THERMOREGULATION AND THERMAL COVER OF DEER AND ELK ON VANCOUVER ISLAND

A PROBLEM ANALYSIS

INTEGRATED WILDLIFE INTENSIVE FORESTRY RESEARCH

A cooperative project between the Ministry of Environment and Parks and the Ministry of Forests and Lands

THERMOREGULATION AND THERMAL COVER OF DEER AND ELK ON VANCOUVER ISLAND

Problem Analysis

F.L. Bunnell

K.L. Parker

L.L. Kremsater

F.W. Hovey

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Victoria, B.C.
V8W 3E7

or

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SUMMARY

1. This problem analysis was requested by the Technical Working Group directing the Integrated Wildlife-Intensive Forestry Research program on Vancouver Island. Its goal is to evaluate research priorities concerning the ways in which intensive forest management will affect thermal cover for deer and elk. It is one contribution to a much larger program examining the interaction of silviculture practices with deer and elk populations.

2. Literature on the potential role of thermal cover is confused or limited by lack of an operational definition, variable patterns in use of cover dependent on meteorological conditions, apparent differences between preference and need, and complete absence of data on the thermoregulatory abilities of black-tailed deer and Roosevelt elk.

3. Objectives of this problem analysis are to review thermoregulatory needs of deer and elk and factors influencing them; to review the influences of forest treatments on factors influencing thermoregulatory needs and thermal cover; to suggest specific studies and priorities; and to suggest methodologies for research.

4. Factors influencing operative temperature and thermoregulation of deer and elk include: air temperature, wetting, wind speed, and components of radiation. The

magnitude of thermal stress on Vancouver Island is unknown, but could be assessed by implementing the research proposed.

5. Forestry practices can influence all abiotic factors determining operative temperature and therefore a stand's suitability as thermal cover. Relationships between forest structure, forestry practices, and components of operative temperature are reviewed.

6. Use of cover will always be influenced by behaviour, but comparison of preference with energetically-defined need provides insights which are useful to management.

7. The subject matter and order of research proposed should document the potential value of, and potential mechanisms for, incorporating provision of thermal cover into forestry practices on Vancouver Island. Under conditions where thermal cover is important, its provision would reduce energy costs to the animal and could increase flexibility of specific stand prescriptions.

SUMMARY OF RECOMMENDATIONS

1. Thermal cover for deer and elk should be defined objectively and metabolically as that vegetative cover which produces an operative temperature such that the animal is in the zone of minimum heat production.
2. The most important research topic, the zone of minimum heat production of black-tailed deer, is essential to a direct, metabolic definition of thermal cover.
3. A second important topic is development of an efficient way to combine abiotic variables (as they are influenced by forest structure) into operative temperature, permitting evaluation of the need for thermal cover and impacts of forestry practices on thermal cover.
4. Preference for cover should be evaluated relative to energetically-defined need. A comparison of preference with need has management implications because it reveals the animals' internal ranking system.
5. Condition indices should be assessed for their potential as integrative measures to evaluate trade-offs between energetic costs and gains.
6. Research on the two major topics should proceed quickly and can be based at the University of British Columbia. Progress on topics of lower priority will involve close cooperation and data sharing with other IWIFR projects.

PREFACE

This problem analysis was prepared for the Integrated Wildlife-Intensive Forestry Research (IWIFR) program being conducted on Vancouver Island by the British Columbia Forest Service and the B.C. Ministry of Environment. The IWIFR program began during 1980, is scheduled to run until spring 1986, and has been allocated a budget of $1.6 million for the 6-year period. The program goal is to carry out a coordinated research program that will provide information needed for the effective integration of forest and wildlife management on Vancouver Island. To promote participation and information exchanges with public and private interests, the Technical Working Group directing the study includes representatives of forest industry and public conservation groups, as well as staff from the two sponsoring agencies and the University of British Columbia. Further information on the IWIFR program is available in annual reports and in progress reports for component studies, available from the Research Branch, B.C. Forest Service or Ministry of Environment, Victoria.

This problem analysis deals specifically with the thermoregulatory needs of deer and elk and the ways in which intensive forestry treatments modify thermal cover. It benefited greatly from rigorous and thoughtful review by Drs. T.A. Black and D.A. Leckenby. It will be followed by a working plan and a series of subsequent studies on aspects of the problem. Other major problem analyses focus on Roosevelt elk and Columbian black-tailed deer, and concern the ways that these species select, use, and respond to various habitats.

A number of short-term and support projects are being conducted during the IWIFR program. Details are available in annual reports for the program.

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1. THE PROBLEM

Following a review of research needs in the broad field of wildlife interactions with intensive silviculture (Ellis 1980)[1], the Integrated Wildlife-Intensive Forestry Research program (IWIFR) was begun. The program's primary objective is to determine how intensive forestry practices influence the ability of forested land to support black-tailed deer (*Odocoileus hemionus columbianus*) and Roosevelt elk (*Cervus elaphus roosevelti*). Problem analyses on the two major species and their habitats (Janz *et al*. 1980; Nyberg 1985; McNay and Davies 1985) have addressed apparent requirements of the species including thermal cover. The importance of thermal cover was described as "rarely...evaluated" (McNay and Davies 1985), "not well understood" (Janz *et al*. 1980) or confused by the question "How can preference be distinguished from need?" (Nyberg 1985).

Because trees and other vegetation mediate the rates of heat exchange between an animal and its environment, silvicultural practices modify thermal cover. As a result, attempts have been made to describe the appropriate forest structure for provision of such cover (Thomas *et al*. 1976; Thomas *et al*. 1979). Silvicultural prescriptions that include provision for thermal cover are necessarily constrained, and constrained by a factor whose importance is "rarely evaluated' or "not well understood". Furthermore, it is apparent that the use animals make of what has been termed thermal cover varies with snow conditions, temperature, and wind speed (Ozoga 1968; Miller 1970; Beall 1974; Leege and Hickey 1977; Leckenby 1977; Euler and Thurston 1980).

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[1] Ellis, R.M. 1980. Problem analysis: intensive silviculture-wildlife interactions: research needs on Vancouver Island. Unpubl. report, B.C. Ministry of Forests.

There are three obvious questions relevant to the general problem of thermal cover as a habitat requirement. First, given the number of factors influencing use of thermal cover and the variability of that cover, can an operational definition of thermal cover be offered? Second, are there ways of assessing the importance of thermal cover to black-tailed deer and Roosevelt elk? Third, are there ways of assessing a forest's ability to provide thermal cover? If these questions can be answered satisfactorily, then it is possible to assess the utility of incorporating thermal cover into silvicultural prescriptions. That assessment would address the primary objective of IWIFR. There are less obvious but still relevant questions. For example, under what conditions can security cover substitute for thermal cover? Such questions become much simpler if a clear conceptual model of thermoregulatory needs of deer and elk can be created. The model should be capable of addressing the three major questions noted.

Problem analyses of three major components of the IWIFR program (deer, elk, and habitat) served to identify confusion surrounding thermoregulatory needs of deer and elk. Research specifically directed to thermoregulation requires specialized skills and equipment which are available within the fourth major component of IWIFR - the researchers working with F.L. Bunnell at The University of British Columbia and supported by the Science Council of British Columbia. This more specific problem analysis has been prepared by the latter group. Its purpose is to identify important issues to be addressed during the study of thermoregulation and thermal cover, and to set priorities for research activities.

2. OBJECTIVES AND SCOPE

2.1 Objectives

The goal of this problem analysis is to create a clear conceptual model of thermoregulation, and to use that model to assess expected interactions between forest treatments and the provision of thermal cover for deer and elk. That process will recommend specific research topics. The objectives that must be met to achieve this goal are:

1) to review the thermoregulatory needs of deer and elk and factors influencing those needs;
2) to review the influence of forest treatments on factors affecting thermoregulatory needs and thereby assess expected impacts of forest treatments on thermal cover (as operationally defined by thermoregulatory needs);
3) to suggest specific studies and assign priorities to each;

and

4) to discuss general methodologies for conducting recommended studies.

2.2 Scope

The treatment concentrates on energy costs of thermoregulation in forested environments. Simple comparisons are made with other energy expenditures to provide relative values and indicate the potential importance these costs have in the animals' annual cycle. The conceptual model that is developed is general for members of the deer family (Cervidae). Efforts are directed to estimating parameters specifically for black-tailed deer and Roosevelt elk but rely heavily on data from other species and subspecies. Examination of the influences of forest structure on micro-meteorological conditions focusses on Douglas-fir stands, but incorporates any data that appear relevant to the conceptual model. Although data are drawn from a variety of sources, discussion of probable relationships is largely restricted to the meteorological conditions prevailing on Vancouver Island and the adjacent mainland. Nyberg (1985) noted the considerable variety in silvicultural treatments and imprecision in managed-stand yield projections on Vancouver Island. The intent of this problem analysis is to treat relationships involving forest cover in a way sufficiently general that a wide variety of silvicultural treatments can be considered.

3. PROBLEM DEFINITION

We recognize three parts to the problem: 1) interactions between the animal and its abiotic environment (Section 3.1), 2) influences of vegetative cover on the abiotic environment (Section 3.2), and 3) influences of forestry practices on those features of vegetative cover that alter the abiotic environment (Section 3.3).

3.1 Thermal Interactions Between Animal and Environment

We begin our treatment of thermal interactions by examining the general nature of thermoregulation and of heat transfers between animals and their environment (Section 3.1.1). Concepts of thermoneutrality and expenditures of energy to regulate body temperature are addressed in Section 3.1.2. This latter section notes the potential importance of these expenditures in areas of relatively mild climates. The third Section (3.1.3) addresses the confusion between preference and need for thermal cover and offers an operational definition that should reduce such confusion.

3.1.1 Heat Transfer and Operative Temperature (Te)

Thermoregulation is the ability to regulate body temperature within acceptable limits despite large variations in ambient conditions. Behavioural, morphological, and physiological adaptations alter the heat exchange between an animal and its environment. This exchange occurs via four modes of transfer: conduction, radiation, and convection of sensible heat and water vapour (latent heat transfer). All four modes are dependent on the temperature gradient between the animal and its environment, its exposed surface area (Morrison 1966; Moen 1973; Chappel 1980), and pelage characteristics (Hammel 1955; Moen 1973).

In addition to these factors, the rate of conduction varies greatly with the thickness of the conducting layer(s), the temperature difference across the layer(s), and thermal conductivity of the layer(s). Up to 30% of the minimum daily heat production in sheep may be dissipated by conduction when lying on cold, poorly-insulated ground (Gatenby 1977). Insulative qualities of snow may actually decrease conductive heat loss to the ground. Convective losses of sensible heat, which are facilitated at low air temperatures and influenced by wind velocity, turbulence, and absorbed radiation, are a major mode of heat loss during winter. Windspeeds up to 10 $m \cdot s^{-1}$ may decrease the effective insulation of bighorn sheep (_Ovis canadensis_) and caribou (_Rangifer tarandus_) by 41-87% (Hart _et al_. 1961; Chappel and Hudson 1978). Radiative heat exchange varies with time of day, degree of cloudiness, substrate emissivity, animal orientation, and body region. Mule deer (_Odocoileus hemionus hemionus_) and elk (_Cervus elaphus nelsoni_) standing in snow and exposed to solar radiation had skin temperatures in winter at an air temperature of -30°C equal to those at +30°C in summer (Parker and Robbins 1984). Evaporative heat loss or latent heat transfer may be cutaneous or respiratory; it varies with the temperature of the evaporating surface, the radiative heat load, respired air temperature and volume, and the vapour pressure difference between the animal surface and the surrounding air. Smaller ungulates tend to dissipate most of their excess heat by panting, as do mule deer, whereas larger animals such as elk depend primarily on sweating (Parker and Robbins 1985). Thermoregulation is the combined action of these processes and is a complex interaction of both animal characteristics and environmental variables.

In most studies, air temperature (Ta) alone has been used to describe the thermal environment experienced by an animal. Air temperature, however, is useful as an index only in thermally simple laboratory conditions and is inadequate when considering heat exchange in the natural environment. Operative temperature (Te) more appropriately describes the effective temperature experienced by an animal (Bakken 1981). It is a biophysical expression that incorporates the thermal consequences of air temperature and incident radiation for a particular animal. Campbell (1977:94) presented the equation:

$$Te = Ta + (re/\rho cp)\,(Rabs - \epsilon\, \sigma\, Ta^4) \qquad (1)$$

where Ta is air temperature, re is an equivalent parallel resistance to convective and radiative heat transfer, ρcp is the volumetric heat capacity of air, Rabs is longwave and shortwave radiation absorbed by the animal, and $\epsilon \sigma Ta^4$ is the longwave radiation emitted by the animal. When the animal's surface temperature is near air temperature $Rabs - \epsilon \sigma Ta^4 = Rni$, net absorbed solar and thermal radiation. For a more complete account of the effects of wind speed and latent heat transport see Campbell (1977: Equation 7.15).

Components within the terms of Eq. 1 include: 1) solar elevation angle which depends on latitude, longitude, and season (Paltridge and Platt 1976; Campbell 1981), 2) direct beam and diffuse shortwave radiation affecting the shadow area of the animal (Wesley and Lipshutz 1976; Campbell 1977, 1981), 3) shortwave and longwave absorptivities of the pelage depending on season (Monteith 1973; Campbell 1977; W.P. Porter, pers. comm.), 4) characteristic dimension which represents the average area over which wind travels on the animal (Campbell 1977), and 5) substrate characteristics and their effect on wind velocity and turbulence. Calculations necessary to estimate Te are summarized in Appendix 1.

Te incorporates the effects of particular combinations of Ta, wind, and radiation into a single variable describing the animal's thermal environment. The same Te can be attained from different combinations of environmental variables. By incorporating all variables into an equivalent temperature, similar to a wind-chill index but also including incident radiation, different habitats may be compared with a common thermal index. Theoretically, a Te determined in the natural environment should evoke similar thermal responses in an animal as the same value of Ta measured in the metabolic chamber (with no solar radiation but similar wind speed). For example, thermogenesis and shivering of animals exposed to extremely cold nighttime winter temperatures cease at morning as direct beam solar radiation is received (Parker and Robbins 1984). At a Ta of -20°C under sunlight on snow-covered surfaces, the operative temperature (Te) experienced by mule deer may be only 0°C, resulting in no increased thermoregulatory response.

In situations in which high wind speeds have an important influence on the thermoregulatory response, an extension of Te, standard operative temperature (Tes) should be employed (Bakken 1980, 1981). The variable of precipitation has not yet been included in the concept of Te, although studies are now examining the theoretical effects of high levels of ambient humidity (Tew) (G.S. Campbell pers. comm.).

3.1.2 Thermoneutrality and Energy Requirements

Although the concept of thermoneutrality has been defined by many, the specific term 'thermoneutral zone' (TNZ) is not self-evident because there are no 'neutral' conditions for the feedback system of temperature regulation (Aschoff 1974). Furthermore, four modes of heat transfer and several biological processes are involved in thermoregulation (Section 3.1.1). Hence, the thermoneutral environment has been analyzed relative to several factors, including: 1) metabolic rate, 2) evaporative heat loss, 3) thermal comfort, 4) preferred temperature range, and 5) animal productivity (Hill 1974). The traditionally accepted definition has been based on metabolic rate (Fig. 1). Other alternatives are difficult to measure because of the subjectivity involved and have received only minimal research. These alternatives, such as comfort zones and preferred temperature ranges, also have important implications to habitat management (see Section 3.1.3).

The range of air temperatures over which metabolic rate of the resting animal is minimal, constant, and independent of environmental temperature is the classical thermoneutral zone or zone of 'minimum heat production' (Fig. 1). Heat production is minimal only for specific conditions (e.g., animal age, season, level of food intake). The lower limit of this zone or lower critical temperature (LCT) depends primarily on the relationships between the animal's heat production and its insulation. Below this limit, the interaction of temperature, radiation, and wind result in environments in which heat losses exceed the minimal heat production of the thermoneutral zone. Metabolic rate and energy expenditure must increase to maintain acceptable deep body temperatures and prevent impairment of tissue function. The upper limit of this zone, or upper critical temperature (UCT), is that temperature above which metabolic rate increases and which is usually associated with hyperthermia. The traditional approach of using metabolic rate

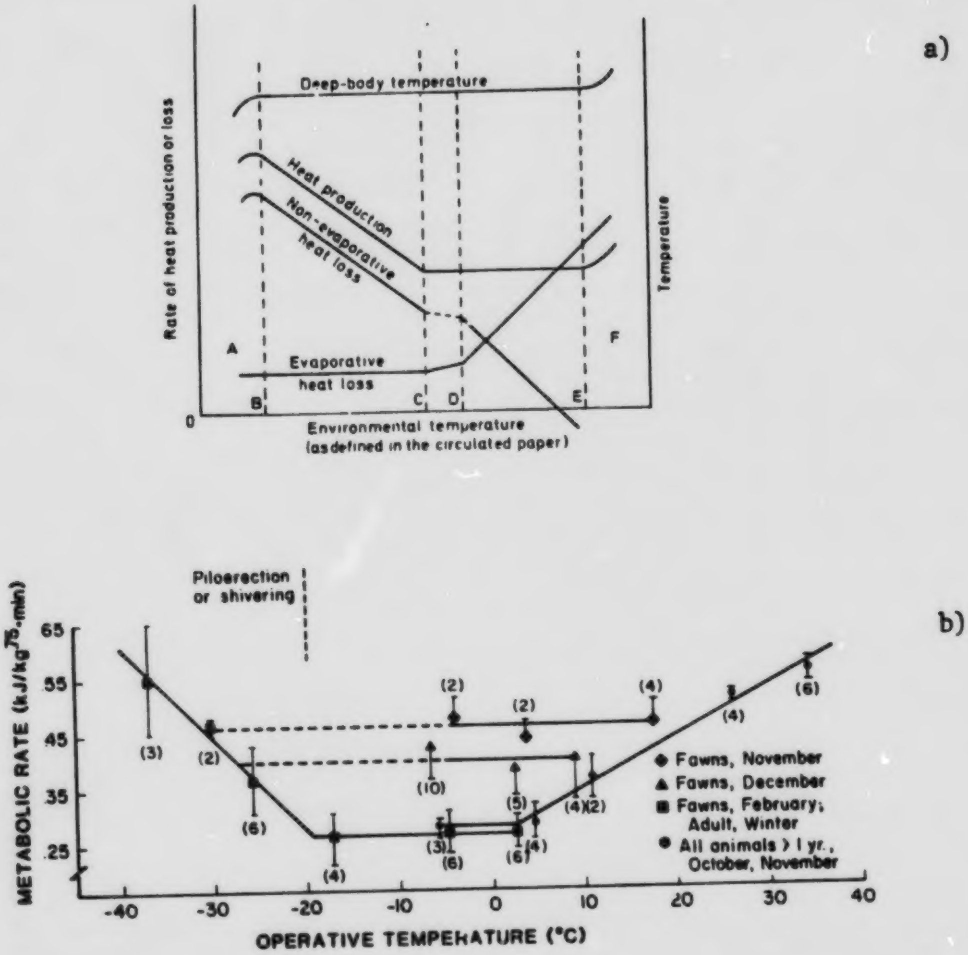

FIGURE 1. Rates of heat production as a function of temperature.
a) Diagrammatic representation of relationships between heat production, evaporative and non-evaporative heat loss and deep-body temperature in a homeothermic animal (from Mount 1974: 438). A: zone of hypothermia; B: temperature of summit metabolism and incipient hypothermia; C: critical temperature; D: temperature of marked increase in evaporative loss; E: temperature of incipient hyperthermal rise; F: zone of hyperthermia; CD: zone of least thermoregulatory effort; CE: zone of minimal metabolism; BE: thermoregulatory range.
b) Metabolic rate of standing, fed mule deer as a function of operative temperature (from Parker and Robbins 1985).

to analyze thermoregulation has been used to define thermal requirements for a variety of captive wild ungulates.

The other four approaches to defining a thermoneutral environment involve animal preference to varying degrees. Evaporative heat loss is used to define the range of temperatures in which metabolic rate is independent of temperature, relatively little heat is dissipated by sweating or increased respiratory ventilation, and behavioural thermoregulation is normally absent (Webster 1974a; Bianca 1974). This zone, termed the zone of 'minimal thermoregulatory effect' is particularly difficult to define in well-insulated animals. Alexander (1974) noted the difficulty when considering an increase in respiratory rate of 20 breaths/minute to 40 breaths/minute in sheep. The elevated rate would increase evaporative heat loss, but is minimal when compared with the sheep's capability of 400 breaths/minute. It is thus unclear what increase in respiratory rate and associated evaporative heat loss must occur before reaching upper limits of the zone of minimum thermoregulatory effort (Fig. 1). Respiratory rate may, however, serve as a better indicator of an animal's state of thermal comfort than does metabolic rate.

The range of air temperatures corresponding to a subjective measure of the sensation of maximum comfort is an animal's 'thermal comfort zone'. A 'preferred thermal environment' or 'temperature range' is one selected by the animal when offered an unrestricted range of environments in, for example, a thermocline. Animal productivity is used to define 'optimum thermal environment' or that environment in which an animal's health is optimum and growth is maximized. This environment may not be optimal for development of thermoregulatory ability. Because an animal's tendency to seek thermal cover may not coincide with metabolic thermal requirements, preferences should be observed carefully. Thermoneutrality is most clearly defined by metabolic rate, but effective management must acknowledge traditional movements and behavioural patterns that may correspond to thermal comfort zones or preferred temperature ranges.

Energy requirements associated with thermoregulation have been defined for a variety of cervids (Table 1), but little is known for black-tailed deer and Roosevelt elk. Resting heat production within the thermoneutral zone has been documented for young black-tailed deer (Nordan et al. 1970) and one study has examined their lower critical thermal environments (Mautz et al. 1985). Data from other cervids provide a relative reference for these two coastal species (Table 1). Based on ecological relationships and geographic distributions, the thermoneutral temperature range for mule deer would be expected to be lower than that of white-tailed deer, which in turn would be lower than that of black-tailed deer. Critical thermal limits of Roosevelt elk may be higher than those of their Rocky Mountain counterpart.

Although several studies of thermally critical

TABLE 1. Thermally critical environments for selected ungulates

Species	Weight	Activity	Feed level	Season	Location	LCT (°C)	UCT (°C)	Source
Mule deer								
(*Odocoileus hemionus*	61.0	standing	ad libitum	winter	Wash.	-20	5	Parker and Robbins 1984
hemionus)	48.7	standing	ad libitum	summer	Wash.	12.5	25	Parker and Robbins 1984
White-tailed deer								
(*Odocoileus virginianus*	65.3[a]	-	fasted	February	N.H.	-10	-	Silver 1973
borealis)	65.3[a]	lying	fasted, fed	winter	N.H.	5	25	Holter et al. 1975
Rocky Mountain elk								
(*Cervus elaphus nelsoni*)	125.0	standing	ad libitum	Jan-May	Alta.	-10	-	Gates and Hudson 1979
	125.0	lying	ad libitum	Jan-May	Alta.	-10	-	Gates and Hudson 1979
	91.7	standing	ad libitum	January	Wyo.	-20	15	Parker and Robbins 1984
	143.5	standing	ad libitum	summer	Wash.	9	-	Parker and Robbins 1984
Red deer								
(*Cervus elaphus elaphus*)	46.0	-	ad libitum	January	Scotland	5	-	Simpson et al. 1978

[a] White-tailed deer body weights estimated from Silver *et al*. 1969.

environments of cervids exist, direct comparison of these can be misleading. An animal's metabolic heat production may be altered by its previous exposure to temperature, level of activity, body posture, plane of nutrition, age, and season. For example, acclimatization to prevailing temperature results in a 9% decrease in metabolic rate in cattle (Webster 1974*b*). Lying postures potentially reduce heat loss through the extremities and may decrease LCT's for moose (*Alces alces*) by more than 10°C (Renecker *et al*. 1978). Fasted pronghorn (*Antilocapra americana*) reached critical thermal environments at air temperatures 12-25°C higher than those on *ad libitum* intake (Wesley *et al*. 1973). Energy expenditures for mule deer fawns decreased 74% between 5 and 8 months of age (Parker and Robbins 1984). Adult mule deer on *ad libitum* intake decreased thermally neutral heat production in winter by 11.5% from summer (Parker and Robbins 1985). Because all these variables can be important, their effects must be accounted for or adjusted to 'standard' conditions in any experimental design, analysis of data, or comparison.

Historically, emphasis has been placed on the lower critical temperatures of ungulates in winter (Table 1). However, as noted by Nyberg (1985), critically low thermal environments for black-tailed deer and Roosevelt elk may never be encountered under thermal regimes as mild as those on Vancouver Island. In this area, more importance should be addressed to animals in summer pelage, particularly in early spring when temperatures may often be less than critically low temperatures (LCT for mule deer = 12.5°C, elk = 9°C) and mid-summer when temperatures may exceed upper critical limits (UCT for mule and white-tailed deer = 25°C). Although summer forage often appears adequate, energy required for thermoregulation is not available for demands of lactation, growth, fattening, and movement. Hence, thermal stress in summer may influence immediate production and future survival (Leckenby 1977). Upper critical temperatures encountered by animals in winter pelage during spring following an energy-demanding winter of decreased forage availability and increased locomotory costs may also be important (UCT for mule deer = 5°C) to survival and reproduction.

The extent to which precipitation contributes to critical thermal environments has not been examined and may be of importance in wet, coastal regions. Prolonged exposures to rain in combination with air temperatures just above freezing almost certainly induce thermal stress in animals in summer pelage and may also affect animals in winter when combined with other energy demands. Young animals are particularly susceptible and may increase metabolic rates to lethal limits when exposed to wind and rain (Hart _et_ _al_. 1961; Alexander 1962). Similarly, precipitation may raise lower critical air temperatures for adult cattle by 15°C (Webster 1974_b_).

3.1.3 Preference Versus Need

Based on observations of free-ranging ungulates purposefully selecting cover, bedding sites, and postures for apparent thermal benefits (Beall 1974; Leckenby 1977), thermal cover is now considered an identifiable, manageable entity of elk and deer habitat. This suggestion by Thomas et al. (1979) and others (e.g., Black et al. 1976) has created much discussion and controversy. Is the observed use of "thermal cover" by free-ranging deer and elk a non-essential, behavioural preference or an actual energy requirement?

An animal appears to have three broad zones of thermal response: 1) indifference, 2) requirement, and 3) buffer. The region of indifference encompasses the range of thermal regimes which have no direct effect on animal activity patterns or energy budgets. The animal is within the zone of minimal heat production but may use cover for other purposes. It is indifferent to the presence of cover relative to thermal requirements. The requirement zone imposes an elevated thermoregulatory cost to the animal; temperatures are greater or less than classical upper and lower critical temperatures, respectively. The buffer zone is that zone in which the animal may seek an ameliorated thermal environment before an elevated thermoregulatory cost occurs if given a choice of different thermal areas. For example, consider the 2-dimensional graph of the effects of temperature and solar radiation on the thermal response of an animal (Fig. 2). It is expected that on a summer

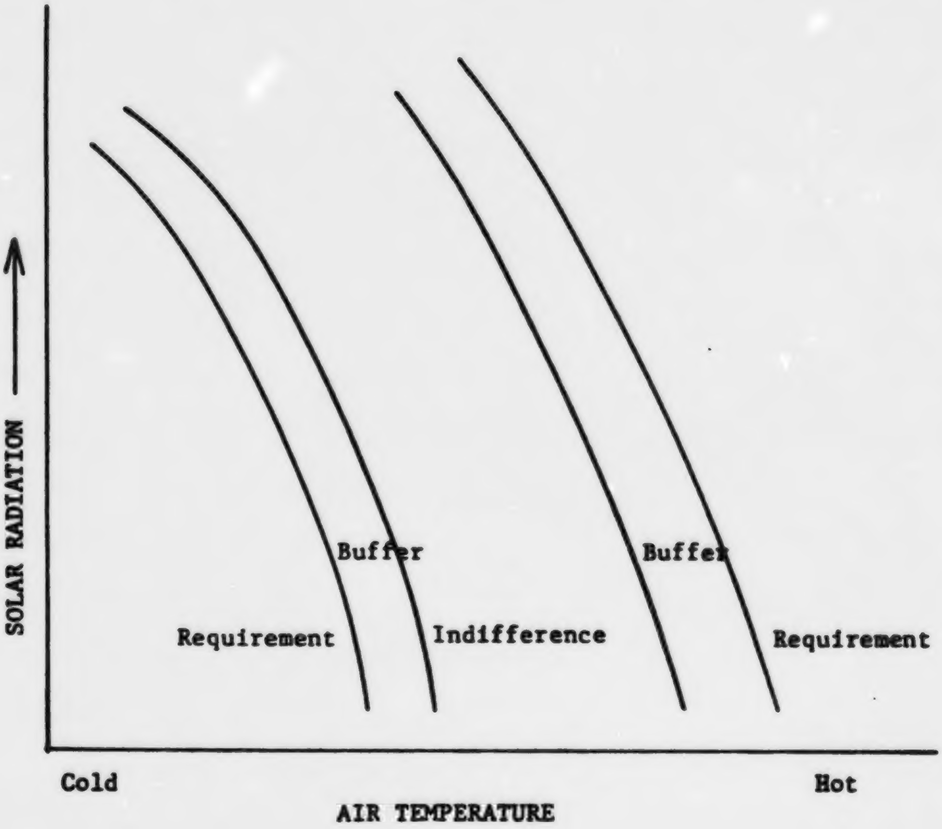
SOLAR RADIATION
Buffer
Buffer
Requirement
Indifference
Requirement
Cold
Hot
AIR TEMPERATURE

FIGURE 2. Estimated zones of thermal response of an animal to the combined effects of solar radiation and air temperature.

day as air temperature and solar radiation levels begin to increase after sunrise, an animal will move into cover before it experiences a thermoregulatory cost. Captive mule deer, black-tailed deer, and elk often purposefully rest in shade or out of the wind during relatively moderate thermal conditions (K.L. Parker, unpubl. data). There is no compelling reason to assume an animal will become uncomfortable by willingly remaining away from shelter if it is not necessary or profitable. Nor is it reasonable to assume an animal cannot sense increasing heat load or thermal drain. The buffer zone differs from the zone of indifference in that changes in heat load modify behaviour. It should be noted that while behavioural decisions in the buffer zone may be made before a thermal energetic cost occurs, animals could have an additional energetic or time cost if shelter-seeking behaviour deprives them of a portion of their habitat , good quality food, or time available for feeding.

Studies on captive animals define the boundary between buffer and requirement zones. They are necessary to determine whether a thermoregulatory requirement as assessed metabolically exists under natural conditions. If it exists, the next question is what is its magnitude and could thermal cover ameliorate the energy requirement? The physiological capabilities of captive ungulates can be applied to free-ranging ones by comparing operative temperatures (Te), ambient water vapour pressures, and wind speeds of different habitats. Field observations in varied habitats where animals are free to make choices are necessary to estimate where the "indifference-buffer" boundary is.

The boundaries between zones are unlikely to be distinct but rather gradations based on the trade-offs between thermoregulatory interactions, behavioural preferences, and food resources. Habitat use patterns are ultimately made in response to total perceived costs and benefits. If the thermoregulatory cost of remaining in the open is counterbalanced by opportunities for increased energy intake, an animal's habitat choice may not directly reflect thermal conditions (Parker and Robbins 1984). Relative to seasonal movements, activity patterns of reindeer (Rangifer tarandus) in winter were more closely correlated with snow depths and forage availability than with air temperatures (Segal 1980). With the greater forage resources of summer, reindeer activity was correlated with changes in air temperatures and solar radiation.

Daily activity patterns are influenced by animal size and heat storage capability. Animals with a low surface area (A) to volume (V) ratio (i.e., large animals) and large thermal resistance across pelage plus tissue are able to endure longer exposures to environments outside acceptable operative conditions (Campbell 1977). Small animals, with high A/V ratios, respond much more quickly to environmental changes and are more restricted by behavioural thermoregulation (Zervanos and Hadley 1973).

A further complication in understanding this trade-off process is that while foraging patterns may be restricted by high ambient temperatures (Luck and Wright 1962; Taylor and Lyman 1967), a tolerance to high effective temperatures is not necessarily correlated with increased grazing time or growth (Finch _et_ _al_. 1982). It is apparent that thermal constraints can play a major role in modifying or determining activity patterns and habitat selection (review of Bunnell and Gillingham 1985), but it is unclear how these effects influence production or survival.

These observations indicate two major reasons for the confusion between preference and need noted by Nyberg (1985). First, we expect an animal to show preference for thermal cover when it anticipates being or is outside its zone of minimum heat production; it may be in a buffer zone (Fig. 2). Attempts to measure that preference and relate it to abiotic variables, however, may frequently be confused by the animal's activities in both the indifference and buffer zones (Fig. 2). Such activity will produce considerable variation in any field measurements. Furthermore, tradeoffs between activities, such as foraging with shelter-seeking, induce additional variation in field observations. Second, a multitude of factors influence the operative temperature of the animal (Section 3.1.1). With appropriate data 'thermal needs' can be defined operationally as those areas of operative temperature in which an animal is outside the zone minimum heat production and must expend additional energy to thermoregulate (Fig. 1). Within those operative temperature regimes the animal needs additional energy. Most field studies have dealt with only a few of the variables contributing to operative temperature. Attempts to relate animals' shelter-seeking to single variables avoid complexity but necessarily increase the variability in any potential relationship. No consistent relationships between single abiotic variables and shelter-seeking by mule deer or elk have been found (D.A. Leckenby and K.L. Parker unpubl.). Furthermore, a tradeoff may still exist - the animal's energy intake while foraging may exceed the thermal need generated by foraging in a thermally unfavourable environment.

Some of the confusion between preference and need can be reduced by an operational definition of thermal cover. The thermoneutral zone is the zone of minimum heat production determined by Te or Tes; the zone is metabolically defined and determined by several interacting abiotic variables. Outside the zone the animal bears an additional energetic cost and needs energy to meet that cost. Some modification of abiotic conditions is necessary to avoid these increased energy expenditures. Thermal cover is thus that vegetation which for any specific combination of abiotic variables permits the animal to exhibit minimum heat production. The definition has a major disadvantage for the forest manager: it suggests that there is no absolute standard or value of thermal cover. Several different kinds of vegetation will produce similar effects, and thermal cover will differ markedly among sets of abiotic conditions. The definition also has three advantages. First, it eliminates the ever-present tradeoffs and behavioural responses that enter definitions based on choices and tradeoffs (but see Section 4.4.3). Second, with appropriate data it is theoretically calculable for any size and nutritional state of animal, combination of abiotic conditions, and structure of vegetation. Third, because it is metabolically defined it can be compared more directly with other energy costs or inputs which should facilitate development of favourable stand prescriptions.

As expressed, the definition of thermal cover is useful to researchers attempting to evaluate the role thermal cover plays in an individual animal's net energy budget or the kind of stand most effective as thermal cover under given weather conditions. It could be extended to treat influences of age or different planes of nutrition, but to be of most utility in management some estimate of desireable herd size and productivity would have to be incorporated. For example, positive energy balances that allow recruitment levels just maintaining a minimum viable population of an unhunted herd will be smaller than energy balances which sustain recruitment rates in a population from which 500 individuals are harvested each year. Thermal cover will be more important to the latter herd, and need should be defined relative to some target level of production or other management objective. Thermal cover sufficient for survival may not be the management objective.

3.2 Influences of Vegetative Cover

The operational definition of thermal cover acknowledges that different vegetative structures modify abiotic components of the Te or Tes experienced by the animal. Vegetative cover can influence each of major abiotic components of Te: precipitation or relative humidity, temperature, wind speed, and radiation. Precipitation is discussed in terms of the throughfall or interception of rain; interception of snowfall was treated by Bunnell *et al*. (1985).

3.2.1 Throughfall And Interception Of Rain

Any canopy has a relatively well-defined capacity to store rainfall falling on it; when this capacity is exceeded further intercepted water either drips from the canopy or runs down stems (Rutter 1975). The combination that drips from the canopy and falls through gaps is usually called throughfall (T); the sum of throughfall and stemflow (Sf) is net precipitation (Pn). The difference between gross or incident precipitation (P) and net precipitation is called interception or interception loss (I). By these definitions gross precipitation is partitioned as:

$$P = I + T + Sf \qquad (2)$$

Our interest is the amount of rainfall that falls or drips from a canopy and could wet deer or elk. We therefore concentrate on throughfall and the relationship:

$$T = bP - a \tag{3}$$

Many studies present results in terms of interception:

$$I = a + (1 - b)P \tag{4}$$

Equations 3 and 4 are equivalent when stemflow is negligible. They have two important features. First, coefficient a is related to storage of water in the canopy and b is related to the evaporation of intercepted rainfall during a storm; both should reflect some attribute of the tree crowns or forest canopy. Second, the relationship between throughfall (or interception) and gross precipitation is linear. The latter may be unclear when throughfall or interception are expressed as percentages of total rainfall. The relationships are then necessarily curvilinear and asymptotic (Fig. 3):

$$I\% = (a + (1 - b)P)/P \tag{5}$$

Reviews of Zinke (1967) and Blake (1975) used this simple regression approach. As an estimate of interception the approach has been criticized (e.g., Rutter _et_ _al_. 1972; Jackson

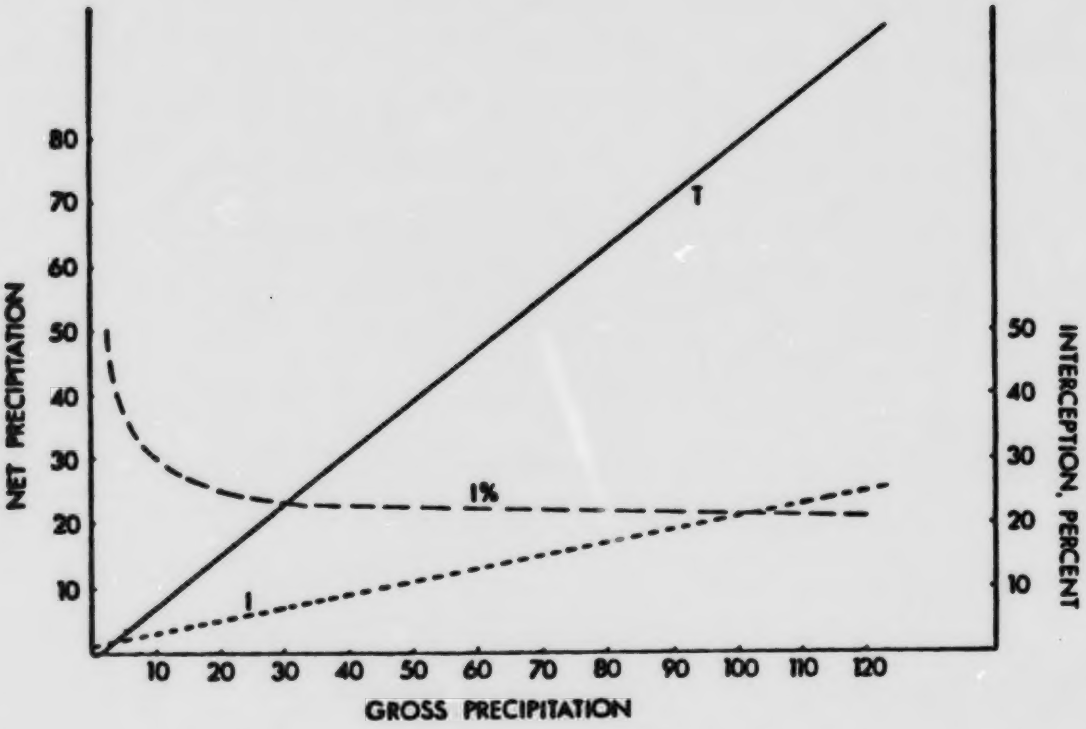

FIGURE 3. Relationship of throughfall (T), interception (I), and percent interception (I%) with gross precipitation when underlying function is T = 0.8P - 0.1.

1975; Rutter 1975) for not accounting for such variables as rainfall intensity and duration, and the drying interval between storms. Recent attempts to incorporate more physical relationships have used complex simulation modeling (Rutter et al. 1972) or complex regression analyses (Gash 1979) of hourly meteorological data. The reliability of simple regressions to estimate canopy storage also has been criticized (Leyton et al. 1967; Rutter et al. 1972), primarily because smaller storms do not fully wet all canopy surfaces and fill canopy storage, or evaporation is non-zero.

For many questions involving thermal cover there are three good reasons for retaining a simple regression approach. First, regressions of throughfall on storm size for a given stand commonly yield values of r^2 greater than 0.90 (e.g., Niederhof and Wilm 1943; Rogerson 1967; Giles et al. 1985). Second, the theoretical arguments of Leyton et al. (1967) that storage capacity is better estimated by choosing storms such that coefficient $b = 1.0$ (evaporation is zero) can be misleading. There is no compelling reason to believe that b is not also a function of canopy attributes otherwise considered to be represented by coefficient a. Third, arguments that the error term for predicted throughfall is unreliably large (e.g., Rutter 1963; Kimmins 1973; Giles et al. 1985) are not convincing. Error terms estimated from normal distributions give erroneously large errors for non-normal distributions. Frequency distributions of throughfall amount are inevitably skewed (e.g., Ford and Deans 1978), often leptokurtic, and a better approach is to examine the type of distribution obtained (Kendall and Stuart 1977) before calculating error terms. For questions evaluating the general utility of older stands as thermal cover an appropriate approach is to ignore stemflow, relate throughfall simply to gross precipitation ($T = bP - a$), and to consider both a and b a potential indicators of storage capacity.

Questions considering movements of animals over a short period (24-72 h) may have to include changing intensity of rainfall during a storm ($mm \cdot h^{-1}$), or explicitly incorporate evaporation during a storm. Kittredge *et al*. (1941) found that total storm size was a better predictor of throughfall than rainfall intensity for storms up to at least 46 mm. Similar observations were made by Horton (1919), and it is probable that explicit incorporation of intensity is desireable only in large storms lasting several days. During intermittent summer storms, questions addressing detailed movements of animals as a function of thermal cover should acknowledge both rainfall intensity and evaporation explicitly (e.g., Rutter and Morton 1977). In such cases, the more complex models of Rutter *et al*. (1972) and Gash (1979) are appropriate.

Analytical treatment can be limited to throughfall and interception only by omitting stemflow. Such omission appears important only in young stands or for species whose branches project upwards away from the trunk. The percentage of gross precipitation represented by stemflow has been reported at 16.6% in beech (Fagus silvatica, Delfs 1967), 20.8% in young Scotch pine (Rutter 1963), and 27% in a 14-year-old Picea sitchensis plantation (Ford and Deans 1978). Evaluations of throughfall in younger stands should subtract stemflow (Sf, mm) from gross precipitation. An appropriate general relationship has the form:

$$Sf = cP - d \tag{6}$$

Several authors provide such regressions (e.g., Kittredge et al. 1941; Wilm and Niederhof 1941; Zinke 1967; Rutter et al. 1975); the coefficients have been found to vary with basal area, crown area, dbh^2, and relative height of adjacent trees (Hoppe 1896; Kittredge et al. 1941; Wicht 1941; Rutter 1963). In older stands of trees with naturally pendant branches stemflow is unimportant and usually less than 1% of total precipitation (Rothacher 1963; Patric 1966; Delfs 1967; Spittlehouse and Black 1981). One biological implication is that ground near trunks of young trees, or trees with upright branches, accumulates water and is unattractive for bedding.

Among mature, coniferous forests in western North America throughfall generally differs little (60 to 80%, Table 2). Regardless of stand type the amount of throughfall increases linearly and the percent asymptotically with storm size (Fig. 4; note that by ignoring stemflow in Fig. 4, % interception = 100%

TABLE 2. Throughfall of rain in western coniferous forests

Predominant species	Throughfall (%)	Regression equation[a]	Source
Western white pine and hemlock	79	-	Minns et al. 1933
Lodgepole pine			
Virgin, 11.8 M bd ft/acre	69.1	$T = 0.805P - 0.029$	Niederhof and Wilm 1943
8 M bd ft/acre	80.8	$T = 0.868P - 0.015$	
4 M bd ft/acre	85.1	$T = 0.906P - 0.013$	
2 M bd ft/acre	86.5	$T = 0.893P - 0.007$	
Clearcut (all trees > 9.5 in dbh removed)	92.8	$T = 0.99P - 0.015$	
Douglas-fir	66	-	Simson 1931
25-yr-old Douglas Fir	57+	-	
Sitka spruce and western hemlock:			
valley	61	$T = 0.607P + 0.003$	Issac 1946
ridge	69	$T = 0.655P + 0.03$	Issac 1946
Douglas-fir	76	-	USFS 1957
Douglas-fir (age 70 yrs)			
100% crown closure	70[b]	$T = 0.78P - 1.84$[c]	Giles 1983
60% crown closure	92[b]	$T = 0.96P - 0.85$[c]	
Douglas-fir			
21-yrs-old, 1840 stems/ha, 9 m tall, LAI = 7.2	81[d]	-	Spittlehouse and Black 1981
25-26 yrs old, 820-840 stems/ha, 12.5 m tall, LAI = 5.0	76-77[d]	-	
Douglas-fir and associated species	68	$T = 0.653P - 0.16$	Chowdappa 1960
Douglas-fir and associated species	68	-	McMinn 1960
Douglas-fir and western hemlock	76	$T = 0.831P - 0.046$	Rothacher 1963
Western hemlock and Sitka spruce	73	$T = 0.77P - 0.086$	Patric 1966

[a] T = throughfall (inches per storm); P = gross rainfall (inches per storm).
[b] 100% - interception % as calculated from water balance analysis, Giles *et al*. 1985.
[c] Calculated in mm from interception equations in Giles 1983.
[d] 100% - interception % as calculated from growing season, water balance analysis.

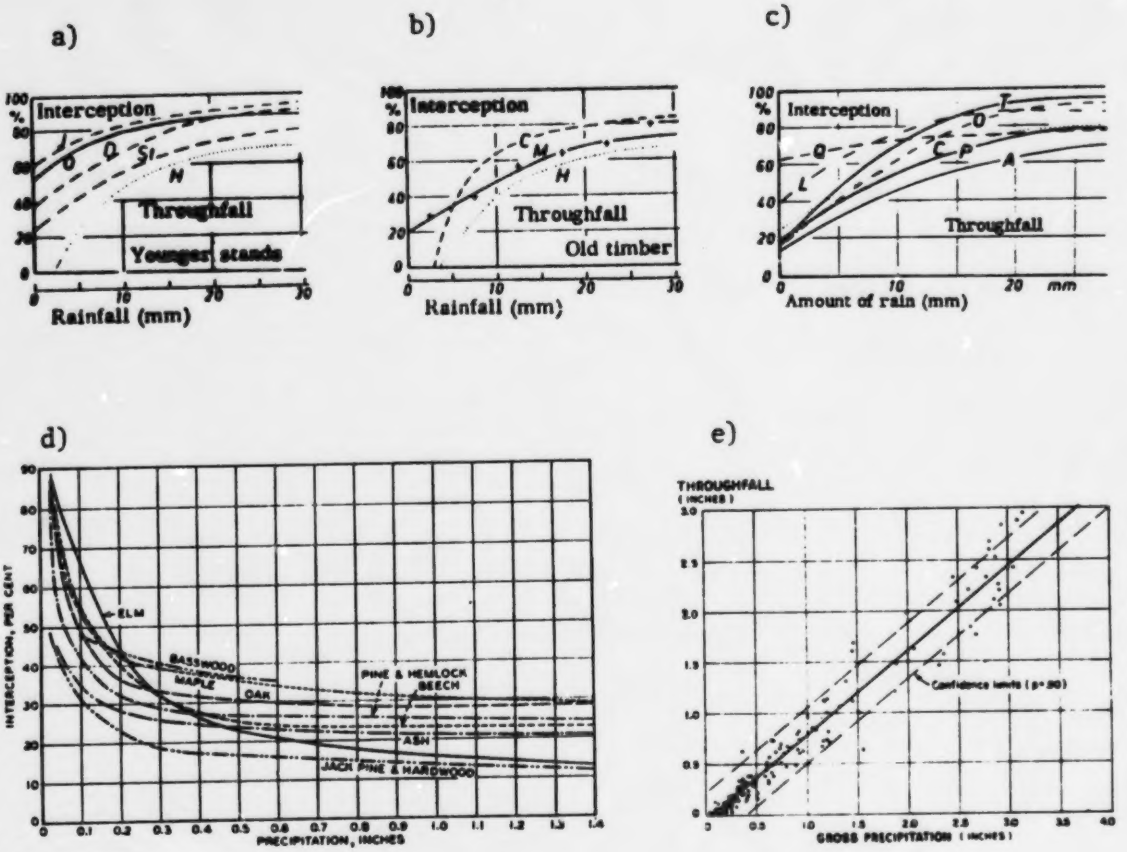

FIGURE 4. Throughfall and interception of rain in forests as a function of storm size.
a) Throughfall of rain in young Abies stands. Ages: J = 15 years old; O = 35-50 years; D = 30 years; St = 60 years; H = 40-60 years (from Geiger 1966: 332).
b) Throughfall of rain in old Abies and Pinus stands. C = 'California pine'; M and H are 60 and 40-60 year old Abies stands, respectively (from Geiger 1966: 332).
c) Throughfall of rain and snow in winter. Q = Quercus rubra; L = Larix eurolepsis; T = Thuja plicata; O = Picea omorica; C = Chamaecyparis lawsoniana; P = Pinus nigra; A= Abies grandis (from Geiger 1966: 336).
d) Interception of rain corrected for stem flow except for jack-pine and hardwood (from Kittredge 1948: 104).
e) Throughfall in mature Douglas-fir during summer storms (May-September) (from Rothacher 1963: 428).

- % throughfall). For very light storms, or during initial stages of a storm, throughfall is almost 0%, particularly in older stands (Fig. 4b,d,e). Throughfall increases rapidly from near 0% in showers less than 2.5 mm to about 60 - 80% in showers greater than 10 mm; it stabilizes at 80 to 90% in larger showers (Fig. 4). Pronounced effects of tree species are not evident even under the same precipitation regime (Table 3).

Because storage capacity is more quickly attained in the more intense storms of winter, there is a pronounced seasonal effect on throughfall. In old-growth stands dominated by Douglas-fir, Rothacher (1963) found the average throughfall during winter storms was 86.3% (e.g., Table 4) but only 70.8% during summer. Similar differences between seasons associated with intensity of precipitation have been documented by others (McMinn 1960; Helvey and Patric 1965; Delfs 1967). Generally, throughfall that could reach deer or elk is significantly greater in the winter. A given stand's potential to provide thermal cover by reducing wetting is thus greater in summer than in winter.

Stand attributes that influence throughfall should be those reflecting canopy storage. Using the simple regression relationships treated here, Zinke (1967) found that storage capacities of coniferous forests during rainfall mostly ranged from about 0.5 to 2 mm. Similar values for storage capacity (coefficient a of Eq. 3) are found in Table 2. The concern of Leyton et al. (1967) and subsequent workers (e.g., Rutter et

TABLE 3. Throughfall of rain in stands of different tree species (data of Ovington 1954)

Description of saplings				Quantities measured		
Type of tree (all 22-23 yr old)	Height of stand (m)	Height of canopy (m)	Length of crown (m)	Throughfall (%)	Stem flow (%)	Drops
Deciduous						
Q[a] *Quercus rubra*	7.3	2.4	4.9	68 - 71	0.3	68
Coniferous						
L *Larix eurolepsis*	14.6	3.0	11.6	70 - 90	0.1	45
T *Thuja plicata*	7.6	2.1	5.5	63 - 65	0.1	46
O *Picea omorica*	10.1	4.0	6.1	59 - 61	0.2	66
C *Chamaecyparis lawsonia*	8.8	1.8	7.0	56 - 57	0.1	48
P *Pinus nigra*	8.5	2.1	6.4	52 - 53	0.2	61
A *Abies grandis*	14.3	4.9	9.4	52 - 64	0.1	64

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[a] Letters refer to Figure 4c.

TABLE 4. Average throughfall in mature Douglas-fir stands as a function of storm size during November through March (modified from data of Rothacher 1963: 429)

Precipitation class (cm)	Storms (number)	Average throughfall (%)
5 - 10	5	88.4
10 - 15	4	92.9
15 - 20	6	88.4
over 20	4	95.7

TABLE 5. Annual and summer throughfall of rain in conifer stands of different height ranges (data of McMinn 1960 modified from Zinke 1967: 151)

	Height	Throughfall (%)	
Species	(m)	Annual[a]	Summer
Douglas-fir	60.7 - 73.2	56	43
Douglas-fir	44.8 - 53.3	69	51
Douglas-fir	26.2 - 35.4	72	61
Western red cedar	38.1 - 59.7	67	60

[a] Data averaged over 5.5 years.

al. 1972; Gash 1979) have had with this approach to estimating storage capacity is best illustrated graphically (Fig. 5). Values of gross precipitation of less than 0.1 in (2.5 mm) were insufficient to ensure complete saturation of the canopy; a line through only the higher values of net precipitation for any given value of gross precipitation had a slope near 1.0 (Fig. 5). The argument for using a line fit through only the highest values of net precipitation or throughfall is that lower values indicate evaporation during the storm and that canopy saturation was not complete. The approach has some theoretical appeal and obvious utility in that a slope of 1.0 assigns all influences on canopy storage to coefficient a. Storage capacities estimated for coniferous canopies by this approach are, however, about the same as estimated by simple regression over all storms (0.8 to 2.1 mm; Rutter et al. 1972; Rutter 1975; Gash 1979). Furthermore, because of the potential effects of wind (drying) associated with storm size, both coefficients a and b could reflect canopy storage. Assigning all effects of canopy storage to one coefficient is important to a treatment of water balance, but not to attempts to relate throughfall to stand attributes.

Canopy storage and throughfall should be related to the projected leaf area index (LAI) of tree crowns and thus should be reflected in such stand measurements as height, crown closure, and basal area. There appear to be few species-specific effects among conifers (Tables 2 and 3) and apparent effects of stand

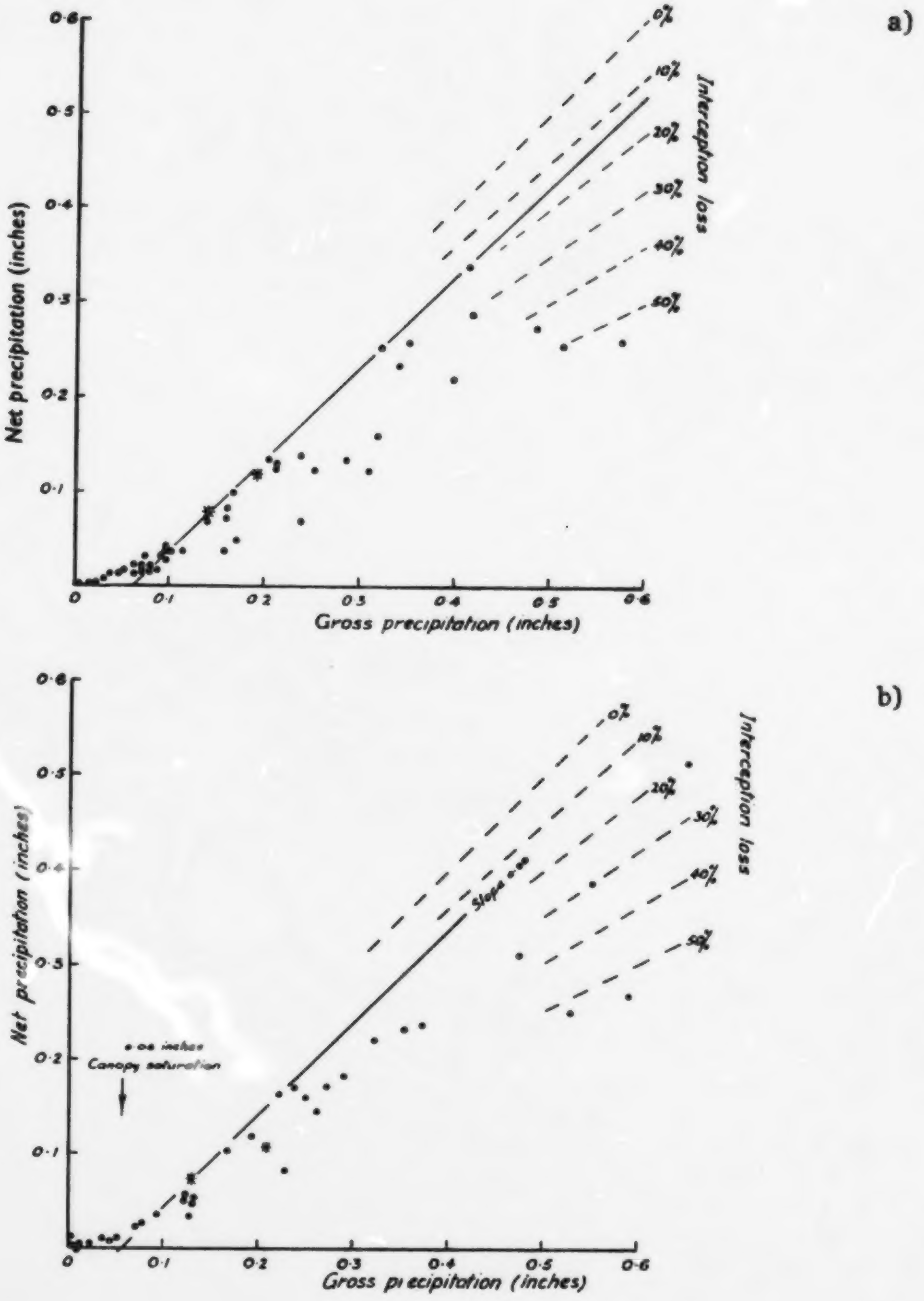


FIGURE 5. Net precipitation (throughfall) as a function of gross precipitation in Norway spruce (Picea abies) plantations. The solid line indicates conditions when the canopy is saturated and little or no evaporation is occurring.
a) 22-year-old plantation (from Leyton et al. 1967: 171).
b) 23-year-old plantation (from Leyton et al. 1967: 173).

age on throughfall primarily reflect age-related differences in crown length and foliage density or total LAI. Age does influence stemflow because younger branches project higher above the horizontal away from the trunk (Cochrane and Ford 1978), and conduct more water towards the trunk (Ford and Deans 1978). Commonly net precipitation decreases with stand age (e.g., Delfs 1967), as stemflow stabilizes at low levels and age-related crown attributes modify throughfall.

In old-growth, Douglas-fir stands of varying height, throughfall decreased with increasing stand height (Table 5). Values for western red cedar were comparable to those for Douglas-fir of the same height range. There are two reasons for the reduction in throughfall with increasing stand height. First, stand height probably reflects length of crown and thus storage capacity. Second, as stand height increases there is an increase in roughness length (Zo) and for a given windspeed a reduction in the resistance to transport of water vapour from the canopy surfaces to the air above (Rutter 1975). As a result drying rates increase with height of the canopy and water is removed more rapidly from potential storage (the storage capacity is extended). This effect of height is likely to appear in coefficient b of Eq. 3.

Crown closure also influences throughfall. Throughfall of summer rainfall declined from 66% in mature Douglas fir with 65% crown closure to 57% in a 25-year-old stand with dense canopy (Simson 1931). Similar effects of crown closure have been documented for mature Jeffrey pine (Table 6) and are evident in the data of Niederhof and Wilm (1943) and Giles (1983) in Table 2. Note that in the latter two cases coefficient a (storage capacity) decreases with decreasing crown closure. Two workers have attempted to separate the effects of crown closure using regressions of the form:

$$T = bP - a - cMCC \tag{7}$$

where MCC is some measure of mean canopy completeness (*sensu* Bunnell *et* *al*. 1985). Working in *Juniperus* woodland in Arizona, Skau (1964) obtained:

$$T = 0.865P + 0.044 - 0.216\ MCC \tag{8}$$

where MCC is a proportion, 0.0 to 1.0. In 25-year-old loblolly pine plantations (*Pinus* *taeda*) Rogerson (1967) obtained:

$$T = 0.877P + 0.13 - 0.00178\ MCC \tag{9}$$

where MCC is the sum of projected crown areas of all trees as a percent of plot area and can exceed 100%. When converted to a common basis, coefficient c is similar for both studies and suggests a decrease in throughfall of 0.9 to 1.1 mm with a 20% increase in crown closure.

In 28- to 35-year-old plantations of several conifer and

TABLE 6. Relationship between interception of rainfall and crown closure for various shower intensities in mature Jeffrey pine (data of Munns, modified from Kittredge 1948: 110)

		Throughfall (%)		
Rain per shower, mm	At base of tree	Under heavy crown	Under light crown	Under edge of crown
0.01 - 0.25	0	0	0	19
1.5 - 2.5	6	16	32	52
2.8 - 7.6	26	52	73	95
12.95 - 25.4	47	67	84	96

hardwood species Aussenac (1968) obtained relationships of the form:

$$\ln(T+1) = a + bEr + cP - dP^2 \qquad (10)$$

where Er is relative illumination (light under the canopy relative to light in the open, %), and T and P are as before. Throughfall increased with relative illumination; the degree of relative illumination had a greater effect at larger storm sizes. Aussenac obtained r^2 values consistently greater than 0.90, suggesting a strong influence of crown closure.

Diameter and basal area also are related to throughfall in young stands (Rogerson 1967; Butcher 1977). Rogerson (1967) obtained the relationship:

$$T = 0.877P + 0.0891 - 0.00101BA \qquad (11)$$

$$(r^2 = 0.9903)$$

where BA is basal area as square feet per acre. This equation assumes that basal area affected the intercept but not the slope of the basic throughfall-rainfall relationship, but the slope of the relationship does change with basal area. To incorporate the change in slope Rogerson calculated:

$$T = 0.980P - 0.0184 - 0.0097(BA \times P) \qquad (12)$$

$$(r^2 = 0.9933)$$

Equation 12 is a significant improvement ($P < 0.01$) over Equation 11 using rainfall alone. There is no obvious relationship between diameter or basal area and throughfall in older stands (Rothacher 1963). The lack of relationship in older stands apparently results from canopy closure remaining relatively static while the stand continues to increase in basal area.

Besides these empirical relationships with basal area, there is a further reason for considering diameter measurements as estimators of throughfall, particularly in young stands. Storage capacity of the canopy in mm is about 0.2 LAI (Rutter 1975); of the stand attributes that are surrogates for LAI, diameter is the most reliable. Giles (1983) estimated total leaf area index by first calculating leaf biomass from dbh relationships (Waring _et al_. 1978) and then converting leaf biomass to total LAI using relationships of Gholz _et al_. (1976). The coefficients a and b of the throughfall relationship (Eq. 3) were well correlated with total leaf area indices estimated from dbh ($r^2 = 0.94$ and 0.97, respectively).

In summary, major influences on amounts of throughfall are storm size and stand attributes that influence canopy storage capacity, such as stand height, crown closure, basal area, and total projected LAI. The latter can be estimated from dbh, at least in younger stands. These attributes are similar to those noted by Bunnell _et al_. (1985) as being important to the interception of snow. Generally, tree species and stand age are of lesser importance. Age of stand is important only in that stemflow should be treated explicitly in younger stands, and basal area and LAI may be better predictors of throughfall in younger (<35 years) than in older stands. Simple regression models appear to estimate throughfall and stemflow reliably and can incorporate potential effects of crown closure, basal area, or LAI.

3.2.2 Temperature

Temperature is a major abiotic variable governing heat exchange between animals and their environment (Section 3.1.1). Air temperature rises more rapidly in the morning than it falls in the afternoon and maximum air temperature lags after solar noon (Fig. 6a). When vegetation is absent or short, summer daytime temperatures decrease logarithmically with increasing distance from the ground surface (Fig. 6b); the relationship is most simply expressed:

$$dt/dZ = aZ^{b} \tag{13}$$

where t is temperature, Z is height, and a and b are coefficients. This can also be expressed:

$$\log(\text{lapse rate}) = \log a + b \log(\text{height}) \tag{14}$$

Under sunny skies at midday b approximates -1.0 and temperature

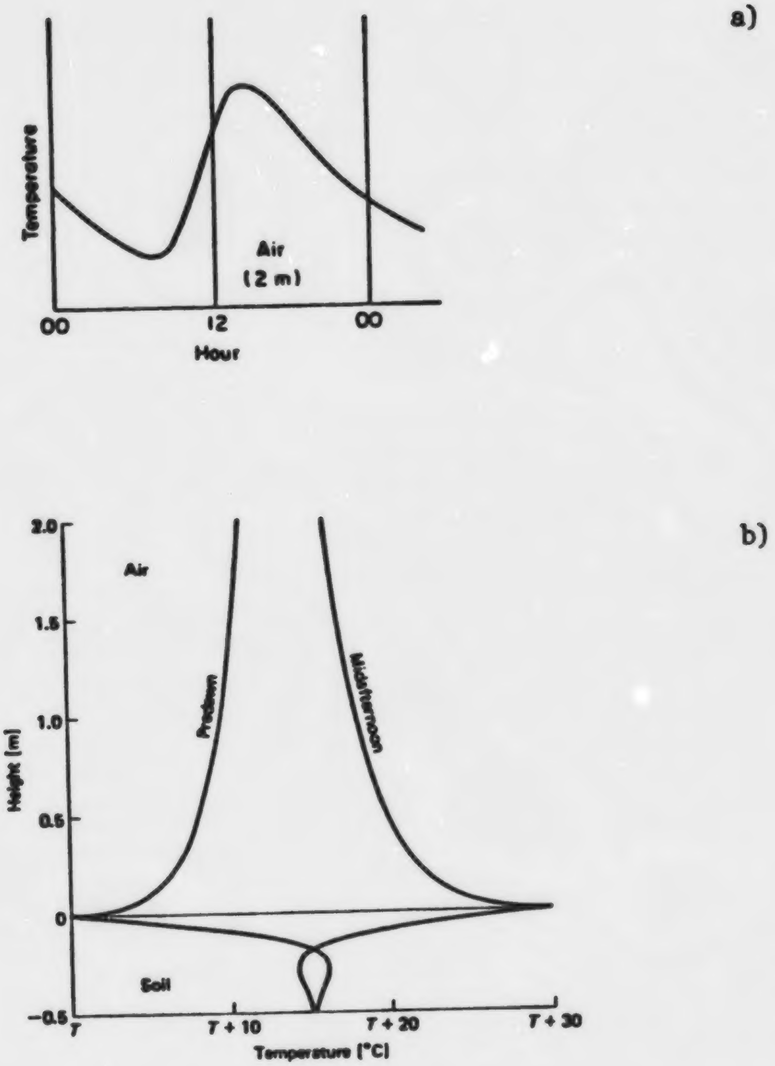


FIGURE 6. Generalized patterns of air temperature (Ta).
a) Air temperature 2 m above the ground on a clear, sunny day (from Lowry 1969: 33).
b) Hypothetical temperature profiles just above and just below the soil surface on a clear, calm day (from Campbell 1977: 10).

is nearly a linear function of the logarithm of height. Under these conditions, if at height Z_1 temperature has a value t_1, then:

$$t = t_1 + a \ln(Z/Z_1) \qquad (15)$$

In the range of deer or elk heights (2 cm to 2 m) the temperature differential is commonly about 5°C for a normalized lapse rate of about 250°C/100m (Lowry 1969). Temperature increases with height when the sensible heat flux is negative (towards the soil surface) and decreases with height when sensible heat flux is positive (away from the soil surface). During daytime sensible heat flux is usually positive, except when there is sensible heat advection (horizontal transport) from a dry, upwind surface (e.g., bare clearcut). To calculate Te for an animal this temperature profile must be known (App. 1).

Forest cover modifies the temperature gradient (Fig. 7) and radiation near the forest floor. By raising the height of the most active radiant surface, forest cover reduces the steepness of the temperature gradient (temperatures are always highest just above the dense crown surface and lowest near the ground surface). With increasing depth and density of the canopy more radiation is intercepted. Interception of incoming solar radiation reduces summer maximum temperatures below the canopy; interception of outgoing longwave radiation increases the minimum temperature under a canopy compared to that in the

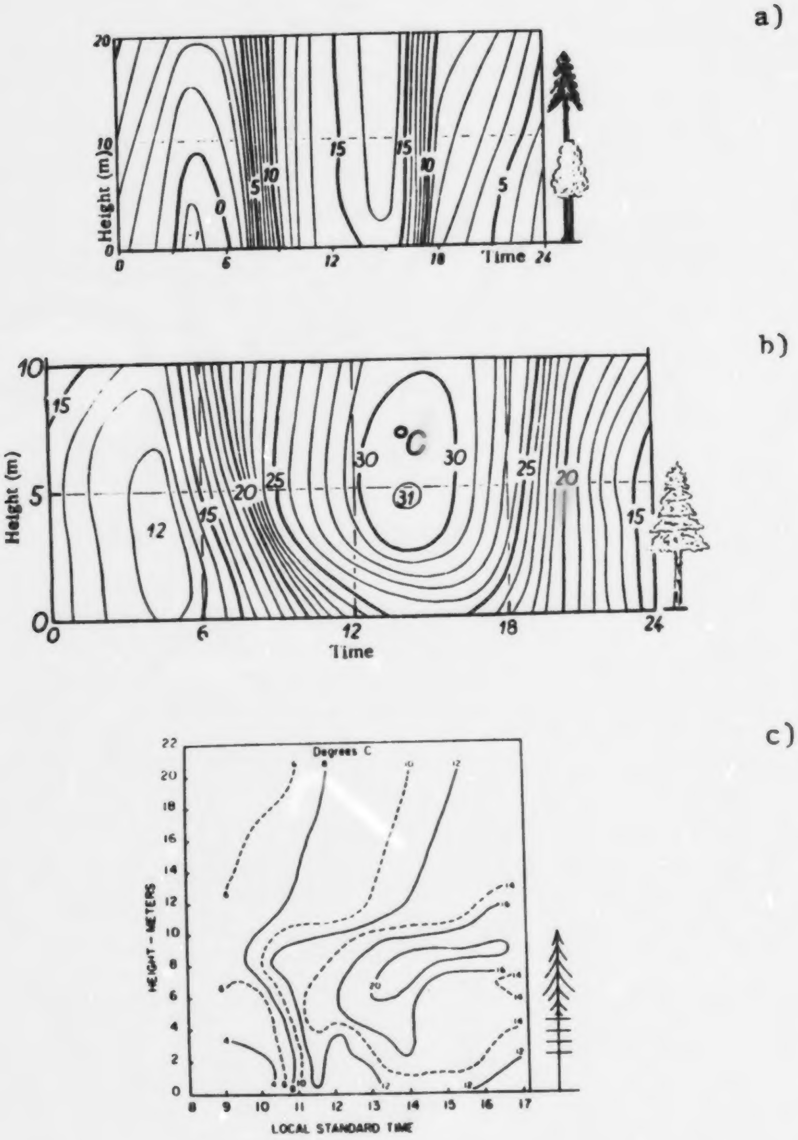


FIGURE 7. Variation of air temperature (Ta) with time and height in forested stands.
a) Variation in a thin pine wood (P. silvestris). (from Geiger 1966: 319).
b) Variation in a dense, young fir plantation (A. alba). (from Geiger 1966: 320).
c) Variation in a pine stand (P. contorta). The tree profile shows total height, live foliage (slanting lines), and dead branches (parallel lines) of the average tree in the stand. (from Bergen 1971: 318).

open (Table 7). In a pine stand (P. silvestris) during summer, surface radiative temperatures below the canopy averaged 2° to 3°C cooler during the morning and 5° to 6°C cooler in the afternoon than those above the canopy (Mukammal 1971). Monthly minimum temperatures may be raised by as much as 3.3°C in January and 3.9°C in July (Table 7). These high values occur when nighttime, outgoing longwave radiation flux in the open is high. Generally, forest cover reduces the range of temperatures (annual, monthly, diurnal) and forests are usually cooler than open areas in summer and warmer in winter (Table 7).

The temperature versus height profiles of Figure 7 are summarized in Tables 8 and 9. The temperature of air in the canopy is quite close to air temperature in the open, whereas vapour concentration is usually higher than that measured at any height above the canopy (Campbell 1981). Such conditions existed in a thinned, Douglas-fir stand near Courtenay, Vancouver Island (Spittlehouse and Black 1981). Because the major effects of forest cover on air temperature are through interception of radiation and modification of windspeed, air temperatures in forests should be influenced by changes in canopy depth and density. For example, a dense fir stand retained greater warmth at night than did a thin pine stand (Fig. 7). Similarly, in very dense canopies, such as unspaced second-growth, there can be significant differences between air temperature in the canopy and the open. Generally, at the height of deer or elk temperatures are cooler than in the

TABLE 7. Influences of forest cover on air temperatures (Ta) (modified from Kittredge 1948: 60)

	Departures, forest from open (°C)			
	Mean maximum		Mean minimum	
Forest type and location	January	July	January	July
Beech climax, N.Y.	-	-4.6	-	+2.5
Western white pine, climax, Id.	-	-3.3	-	+3.9
Western white pine, 2/3 cut, Id.	-	-1.3	-	+2.9
Eastern hemlock, N.Y.	-	-2.7	-	+2.2
Eastern white pine, N.H.	-	-2.7	-	+1.8
Jackpine, 25 yr, Neb.	-0.1	-0.7	+0.6	-1.6
Ponderosa pine, 2100 m, Ar.	-0.6	0.0	+3.3	+2.8
Jeffrey pine, 1830 m, Ca.	+0.4	-0.8	+2.0	+3.7
Aspen-Englemann spruce, 2740 m, Co.	-1.0	-0.6	-0.1	-0.6
Douglas fir, 2740 m, Co.	-1.7	-1.2	+1.2	+1.4
Douglas fir, 2/3 cut, 2740 m, Co.	-0.6	-0.5	+0.7	+0.6

TABLE 8. Temperature and relative humidity in a Scotch pine stand (daily means from Geiger 1966: 321)

Height (m)	0	5	10	15	20
Temperature (°C)	7.1	7.4	8.1	8.4	9.0
Relative humidity (%)	84.0	80.2	79.6	78.4	77.8

TABLE 9. Temperature and relative humidity in a dense fir plantation (from Geiger 1966: 321)

	Temperature (°C)		Relative humidity (%)		
Height of measurement (m)	Daily average	Daily fluctuation	Daily average	Daily fluctuation	Average for overcast days
10.0 above the forest	22.3	16.4	63	58	76
5.0 in tree-top area	21.6	19.4	63	62	80
3.0 in crown area	21.1	19.0	70	62	84
2.5 in trunk area	20.8	18.4	69	60	86
1.5 in area of dead branches	19.6	16.5	71	60	87
0.2 at forest floor	18.3	14.0	79	45	90

canopy, and relative humidities are greater.

The simplest approach to estimating the influence of forest cover on air temperature is to increase minimum temperatures, and decrease summer maximum temperatures by 2°C (Tables 7-9). Height profiles could be approximated from temperatures in the open using a lapse rate of 5°C. For detailed estimates the approach might be unsatisfactory because it fails to incorporate the influences of forest cover on windspeed and radiation which produce much of the variability evident in Figure 7. Generally, the temperature gradient at a particular height increases in magnitude as sensible heatflux from the surface to the air increases, and decreases as wind or turbulence increases. The more complete equation for a temperature profile is:

$$\overline{T} = T_0 - (H/\rho cpku^*) \ln((Z + Zh - d)/Zh) \qquad (16)$$

where $\overline{T}$ is the mean air temperature at height Z, T_0 is the temperature at the exchange surface (Z=d), Zh is a roughness parameter for heat transfer, H is sensible heatflux, ρ and cp are air density and specific heat ($\rho cp = 1200\ Jm^{-3} \cdot {}^{0}K^{-1}$), k is the von Karman constant (0.4), and u* is friction velocity, a windspeed and roughness parameter (Campbell 1977). Because the reference level from which Z is measured is somewhat arbitrary, a correction factor, d, termed zero-plane displacement is used to adjust the profile. The factor d equals 0.0 only for a flat, smooth surface. Note that Eq. 16 is structurally identical to Eq. 15 but differs in explicitly segregating components of sensible heat transfer and turbulence. The more complete equation will do better at expressing the mechanisms by which forest cover modifies temperature (e.g., sensible heat transfer and wind or turbulence). Components are addressed in the following sections on wind and radiation.

3.2.3 Wind

To understand the temperature distribution in the forest, it is necessary to know the wind profile as well as the radiation budget within the stand. The canopy flow regime can be thought of as being divided into three layers (Campbell 1977). The top layer of the flow regime is where drag on the wind above the canopy is exhibited. Wind in this layer flows in the same direction as wind above the canopy and its speed decreases logarithmically with distance down from the top of the canopy. The middle layer is composed mainly of the stem space of the canopy. Here, the wind direction and speed may be quite different from those above the canopy. The lowest layer, close to the ground surface, is characterized by a logarithmic profile similar to that found above the canopy (Fig. 8). For convenience we can consider horizontal speed at any instant as the sum of some basic flow, u, and an additional speed due to eddies, u*. The simplest expression of the wind profile is then:

$$du/dz = (u^*/k)Z^{-1} \qquad (17)$$

or $$u = (u^*/k)\ln(Z/Z_0) \qquad (18)$$

where u is mean wind speed at height Z, u* is friction velocity and is indicative of the amount of turbulence (see Campbell 1977 or Oke 1978), k is von Karman's constant (0.4, dimensionless), and Z_0 is the roughness parameter (dimensions of length). Note that Eq. 17 has the same logarithmic form as that for temperature (Eq. 13). The constant, k, recognizes that turbulent eddies near the surface use about 40% of the room available to them for movement. Most simply, the first two terms represent the manner in which vertical airflow (turbulence) modifies the basic horizontal flow which itself changes logarithmically with height. The logarithmic profile could be expressed:

$$Uz = U_1(Z/Z_1)^a \qquad (19)$$

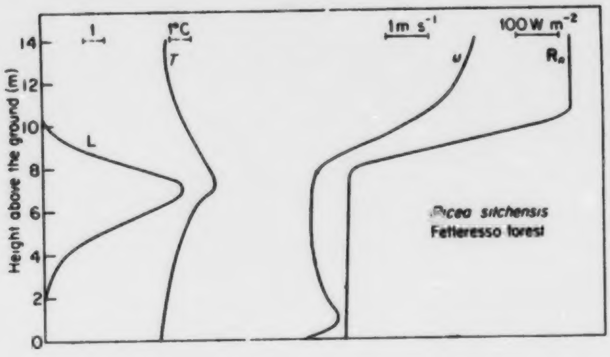
or

$$\log(Uz) - \log(U_1) = a \log(Z/Z_1) \qquad (20)$$

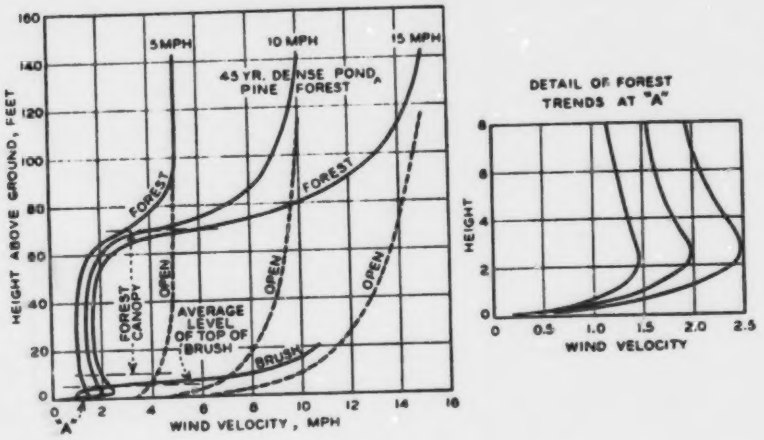
where Uz is windspeed at height Z, U_1 is windspeed at some reference height Z_1, and 'a' expresses something about the intensity of turbulence.

The presence of vegetation modifies the surface roughness

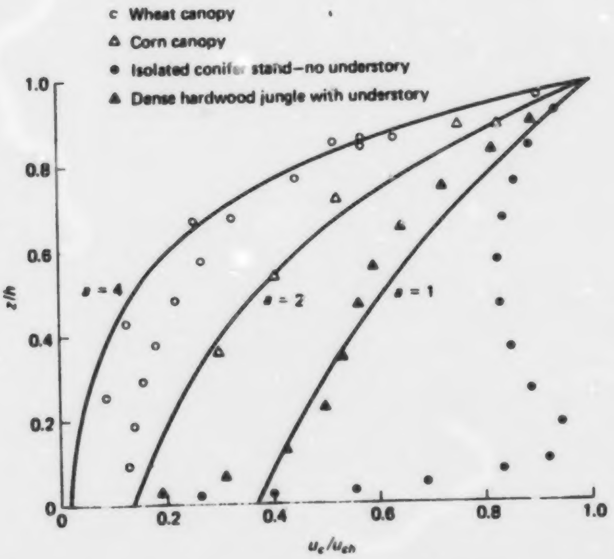
FIGURE 8. Wind speed profiles through different kinds of vegetation.
a) Mean hourly profiles in a *Picea sitchensis* forest for air temperature (T), wind speed (u), and net radiation (R_n); L represents leaf area index of the crown. Properties were measured on a sunny but not completely clear day in July (modified from Monteith 1976: 213).
b) Profiles in *Pinus ponderosa* with and without understory (from Kittredge 1948: 63).
c) Normalized profiles in wheat, corn, conifers, and hardwood jungle: z = height of wind speed measurement, h = height of canopy, u_c = wind speed at height z, U_{ch} = wind speed at top of canopy, a = attenuation coefficient (from Campbell 1977: 43).


Height above the ground (m)
0
2
4
6
8
10
12
14
1
1°C
1m s⁻¹
100 W m⁻²
L
T
u
Rₙ
Picea sitchensis
Fetteresso forest

a)


HEIGHT ABOVE GROUND, FEET
WIND VELOCITY, MPH
5 MPH
10 MPH
15 MPH
45 YR. DENSE POND. PINE FOREST
FOREST
OPEN
FOREST CANOPY
AVERAGE LEVEL OF TOP OF BRUSH
BRUSH
"A"
DETAIL OF FOREST TRENDS AT "A"
HEIGHT
WIND VELOCITY
0
0.5
1.0
1.5
2.0
2.5

b)


○ Wheat canopy
△ Corn canopy
● Isolated conifer stand–no understory
▲ Dense hardwood jungle with understory
z/h
u_c/u_{ch}
a = 4
a = 2
a = 1
0
0.2
0.4
0.6
0.8
1.0

c)

and alters the simple logarithmic profile:

$$U = (u^*/k)\ \ln[(Z + Zm - d)/Zm] \tag{21}$$

or more simply:

$$U(Z) = (u^*/k)\ \ln[(Z - d)/Zo] \tag{22}$$

where Zo is the roughness parameter of the surface or the height at which horizontal windspeed disappears, d is the height of zero-plane displacement (dimensions of length), and Zm, the momentum roughness parameter, explicitly recognizes that the roughness parameters of momentum and heat may differ (see Eq. 16). Generally, the value of Zo increases with height of a homogeneous canopy; the value of d is indicative of the flexibility of the vegetative canopy and represents the height at which the wind speed profile becomes logarithmic (the average height of heat or momentum exchange). Simply, the presence of a vegetative canopy modifies the ability of turbulence to penetrate to the ground and the wind profile is displaced upward by the amount 'd.' Equation 22 does not really imply zero velocity at height $Z - d = Z_0$, because the relationship should only be applied "sufficiently far" above the canopy. Equations 21 and 22 work well above a canopy when lapse rate is adiabatic or neutral (b of Eq. 13 = -1.0; recall temperature modifies turbulence).

Wind speed is reduced in forest stands compared to open conditions (Fig. 8b and c) with the greatest reduction occurring where the canopy and stems are most dense (Fig. 9; Valendik 1964; Gary 1975). For example, in older lodgepole pine stands with few live lower branches wind moved through the stand creating a subcanopy wind speed maximum just below the living crowns (Fig. 9b). In all cases maximum below-canopy temperatures occurred at the height of minimum wind speeds. Generally, wind speeds under a canopy decline relative to windspeeds in the open as the canopy height increases (Fig. 10):

$$Y = 0.912\ X^{-0.6284} \qquad (r^2 = 0.76) \tag{23}$$

where Y is the average wind speed ratio (average speed under canopy/average speed in open) and X is the average canopy height (m). The effect is pronounced and windspeeds under the canopy change relatively little compared to windspeeds above (Fig. 11).

Average canopy height, however, will be useful in predicting wind speed only in so far as it represents canopy foliage distribution with which it is closely correlated (Figs. 8 and 9) and amounts of understory. The effect of understory on wind profiles in a stand is also pronounced (Figs. 8c and 9c). Understory can reduce wind speed significantly, resulting in trunk areas that are cooler by day and warmer by night than in a stand without understory

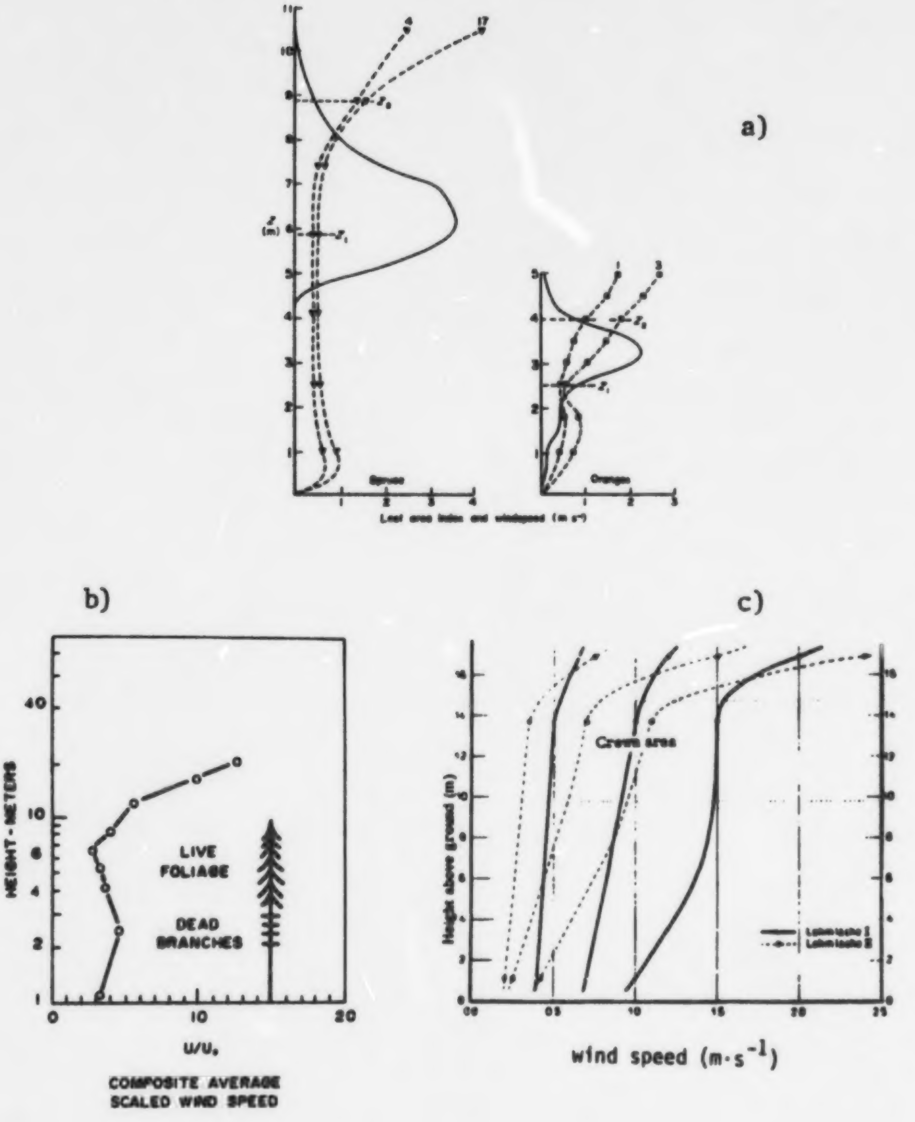


FIGURE 9. Average wind speed profiles as influenced by density of vegetation. a) Profiles within a spruce stand and orange orchard as a function of leaf area index (LAI) (from Landsberg and James 1971: 733). b) Average profile within a lodgepole pine stand. Scaled by u/u* where u = wind speed at height and u* = friction velocity (from Bergen 1971: 319). c) Profiles within Scotch pine stands with (-----) and without (———) an understory of fir (from Geiger 1966: 314).

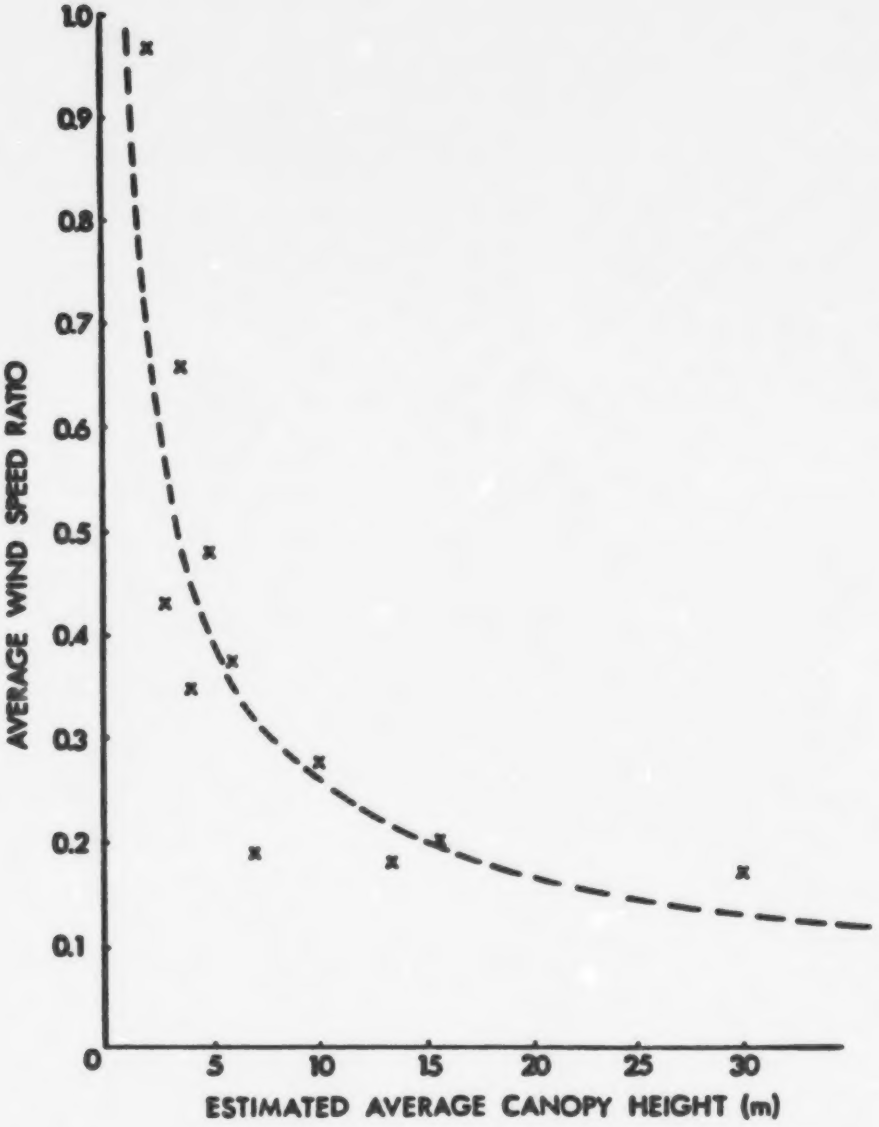


FIGURE 10. Relationship between wind speed ratio (ū in canopy/ū in clearcut) and estimated average canopy height.

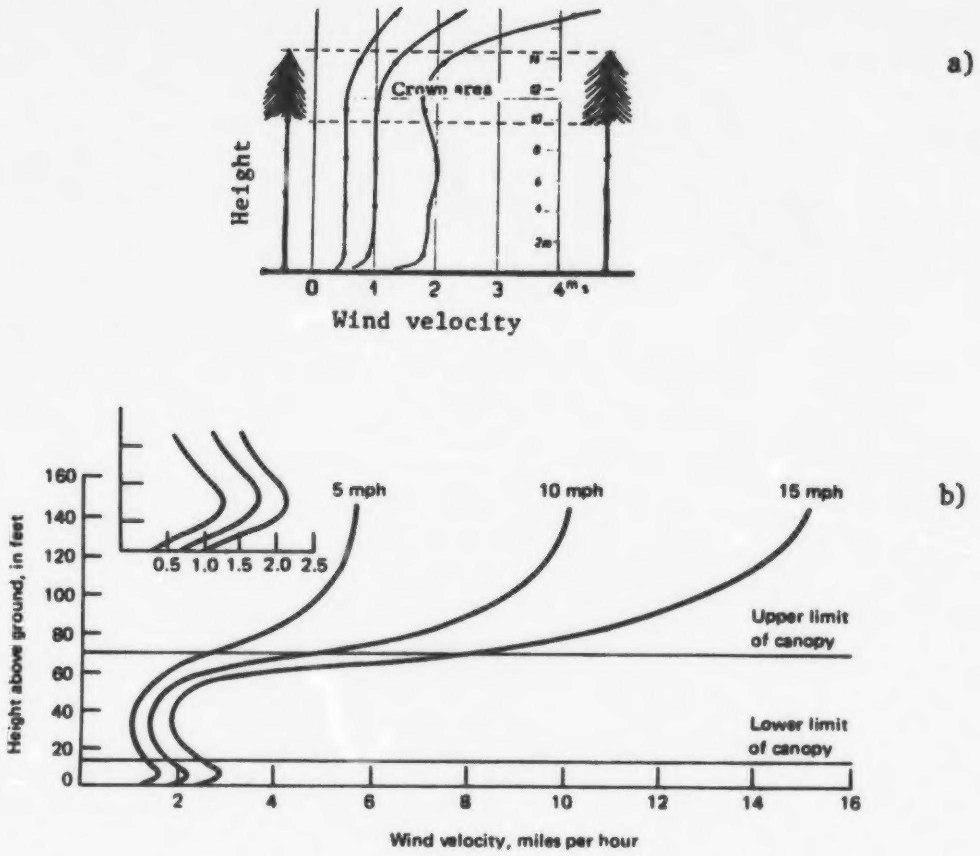


FIGURE 11. Relationship between wind speed within the canopy and wind speed above the canopy.
a) Profiles within a Scotch Pine stand for three different above-canopy velocities (little understory; from Geiger 1966: 312).
b) Profiles within a conifer stand for three different above-canopy velocities (cedar understory; from Smith 1980: 88).

(Fig. 9c). The crown area of a stand with well-developed understory experienced more extreme temperatures than the better-ventilated stand without understory (Geiger 1966:314). An isolated conifer stand with no understory showed very little attenuation of wind speed in the bole area immediately beneath the canopy (Fig. 8c).

Mean horizontal windspeed profiles may not fully reflect the dynamics of wind within a canopy because the vertical momentum flux or drag in canopies is often not proportional to mean horizontal windspeed. Due to the forces of air moving at different wind speeds (e.g., above, within, and below the canopy; Figs. 8 and 9), turbulent eddies are generated. An eddy arriving from above the canopy would be moving faster than air within the canopy and would impart a net increase in velocity or momentum to the lower air. In addition, as wind moves over natural surfaces, friction with the surface generates mechanical turbulence. Thermal turbulence is generated when air is heated at a surface and moves upward due to buoyancy (Campbell 1977). Under turbulent conditions the ability of a medium to transfer momentum is termed the turbulent transfer coefficient or eddy diffusivity, K.

Some estimate of turbulence is necessary to calculate Te (e.g., Eqs. 16 and 21). At the turbulent boundary layer (3 - 5 m above the treetops) vertical momentum flux is proportional to the gradient of horizontal wind speed and well predicted by K theory (see Oke 1978 for a lucid discussion). Within the canopy other transfer mechanisms produce downward transport of momentum against the mean wind speed gradient (Raupach and Thom 1981). Effects of these mechanisms are evident in the bulges in temperature or wind speed profiles beneath the canopy (e.g., Figs. 7, 8, and 9a and b). Relatively little information is available on turbulent flow beneath forest canopies, although some effects are apparent in Figure 12. Vegetation impedes wind flow, reduces wind velocity, and increases turbulence. The value of the K at zero plane displacement, or the distance from the ground to the average height of exchange, (d in Fig. 12) is typically an order of magnitude lower than at the top of the stand where wind speed is greater and solar radiation is received (Monteith 1976). At larger solar angles (1 of Fig. 12) the greater penetration of solar radiation generates more heat and increases thermal turbulence.

Generally, forest cover will reduce wind velocities under a canopy at the level of deer or elk height (Figs. 8 to 11). The reduction will be a function of canopy height (Fig. 10) and structure (Fig. 8 and 9), but will be further modified by understory. Effects of understory illustrated (Figs. 8, 9, and 11) are those of young trees whose canopy merges with that of the overstory; they indicate the potential importance of multistoried stands in creating winter thermal cover. Wind speed in an understory of salal (Gaultheria shallon) is greatly reduced (T.A. Black, pers. comm.), suggesting that taller forms of browse species may provide thermal cover. Effects of forest

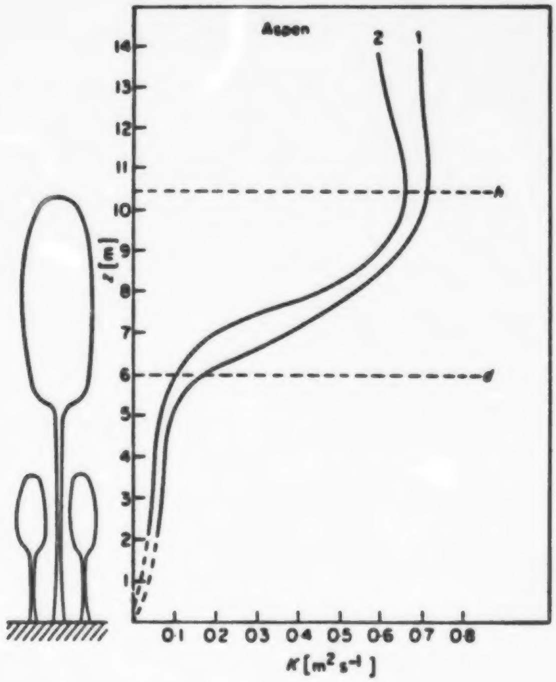


FIGURE 12. Vertical profile of the turbulent transfer coefficient or eddy diffusivity within an aspen canopy at different solar angles: 1 = $\theta > 40^o$; 2 = $\theta < 40^o$; d = zero plane displacement; h = height of stand (from Monteith 1976: 255; see App. 1 for relationship of these parameters to operative temperature).

cover on turbulence are less clear, but will modify the resistance to heat and mass transfer in air for forced convection (Fig. 12, App. 1).

A major problem in estimating the influences of forest cover on the wind speed experienced by deer or elk is that wind speeds at their heights are influenced by both overstory and understory. Simple logarithmic expressions (e.g., Eqs. 17 to 20) work well above a canopy (overstory or understory), additional parameters (e.g., Eqs. 21 and 22) serve primarily to adjust the height at which the profile becomes logarithmic. Beneath a forest canopy the portion of the wind speed profile most significant to thermoregulation may be constrained from below by understory and from above by overstory. Acknowledging these difficulties there are three potential approaches to predicting wind speed at the level of deer height. The simplest uses the empirical relationship of Figure 10 (Eq. 23). The second recognizes the similarity in form of the wind speed profile near the forest floor and above the forest canopy (e.g., Fig. 8b) and uses Eqs. 21 and 22. Within the level of deer or elk height these equations appear generally appropriate, although they usually could not be projected accurately above about 2 m (Figs. 8, 9a, and 9b). Eq. 21 has the advantage of treating turbulence explicitly. For dense understory similar to agricultural crops, d can be estimated from average height (h) as $d = 0.36h$; Zm can be estimated from $Zm = 0.13h$; and Zh of Eq. 16 can be estimated from $Zh = 0.2\ Zm$ (Campbell 1977). These relationships would not hold for a sparse understory. Neither the first nor the second approach incorporates the potential constraints from above by the forest canopy and neither is readily generalized to canopies raised different heights above the understory. The third approach would collate and extract potential empiricisms expressing the form of the near-forest-floor, wind speed profile as a function of normalized canopy height, stratified by two or more understory classes. From inspection (Figs. 8, 9, and 11) below-canopy wind speeds appear to peak at about 50% of the height of the canopy bottom above ground. By collecting constants the relationship can be expressed most simply as:

$$U = c \log (Z/Zo) \tag{24}$$

providing $Z < 50\%$ of the height of canopy bottom above ground. Both c and Zo will vary with the kind and amount of understory present. Data available suggest that if the understory merges with the canopy (Fig. 8c) or the canopy reaches the ground, Eq. 21 will apply at the level of deer or elk height. If the canopy has risen several meters above the understory some expression using the third approach is most appropriate.

3.2.4 Radiation

One of the most important modes of energy transfer between animals and their environment is radiation. Because only a small portion of solar energy is at wavelengths longer than 4 microns (μm) and only a small portion of energy emitted by terrestrial sources is at wavelengths shorter than 4 μm, we can conveniently divide environmental radiation into shortwave (0.3-4 μm) and longwave (4-80 μm). Streams of shortwave radiation received by an animal come: 1) directly from the sun; 2) from solar radiation reflected by sky and clouds; and 3) from solar radiation reflected or transmitted by terrestrial objects (Campbell 1977). The first source is termed direct, the latter two come from all directions and are termed diffuse. It is necessary to separate shortwave radiation into at least these three components because the amounts and directional tendencies are different for each. Total radiant energy available is largely a function of macro-climate, but properties of the forest canopy influence exchanges by emission and reflection. The canopy is a source as well as sink for longwave radiation; the depth of the canopy influences the quantity of shortwave radiation and the relative proportions of direct and diffuse light.

Emission of longwave radiation can be calculated from the Stephan Boltzmann law (radiant flux density = $\epsilon \sigma T^4$; App. 1) provided emissivity is known. Most natural surfaces have emissivities between 0.90 and 0.98 (Campbell 1977) and emissivity of forest canopies is usually taken as unity (Jarvis *et al*. 1976), although it will be slightly less. Dirmhirn (1964) gave a value for coniferous forest of 0.97. Nighttime radiant energy fluxes have been measured under three different cover types during winter. The least amount of downward thermal (or longwave) radiation came from the clear sky, intermediate amounts under hardwoods, and the most under cedar (*Thuja occidentalis*) cover (Fig. 13*a*).

The equations illustrated in Fig. 13*a* are informative (as expressed in Moen 1968:340 the equations are incorrect; σ is omitted). To calculate longwave irradiance from the atmosphere some estimate of atmospheric emissivity is necessary; it is usually estimated from the Idso-Jackson equation: $\epsilon a = 0.72 + 0.005\ Ta$, where Ta is air temperature(°C). Substituting calculated emissivity into the equation of Moen (1968) for an open field reveals poor agreement (Fig. 13*b*). The observation of Campbell (1977) that the Idso-Jackson equation may not work at low temperatures appears justified, and the equation should not be used at temperatures below 0°C. Also illustrated (Fig. 13*b*) is downward longwave irradiance calculated from $\epsilon\ \sigma\ T^4$ assuming ϵ of the cedar canopy is 1.0 and the temperature of the needles is 1°C warmer than Ta. The small, curvilinear departure from observed values likely reflects the change in ϵ with Ta, but agreement is good and indicates a potentially useful approach for calculating radiant flux density under a closed canopy. The difference between the cedar and hardwood

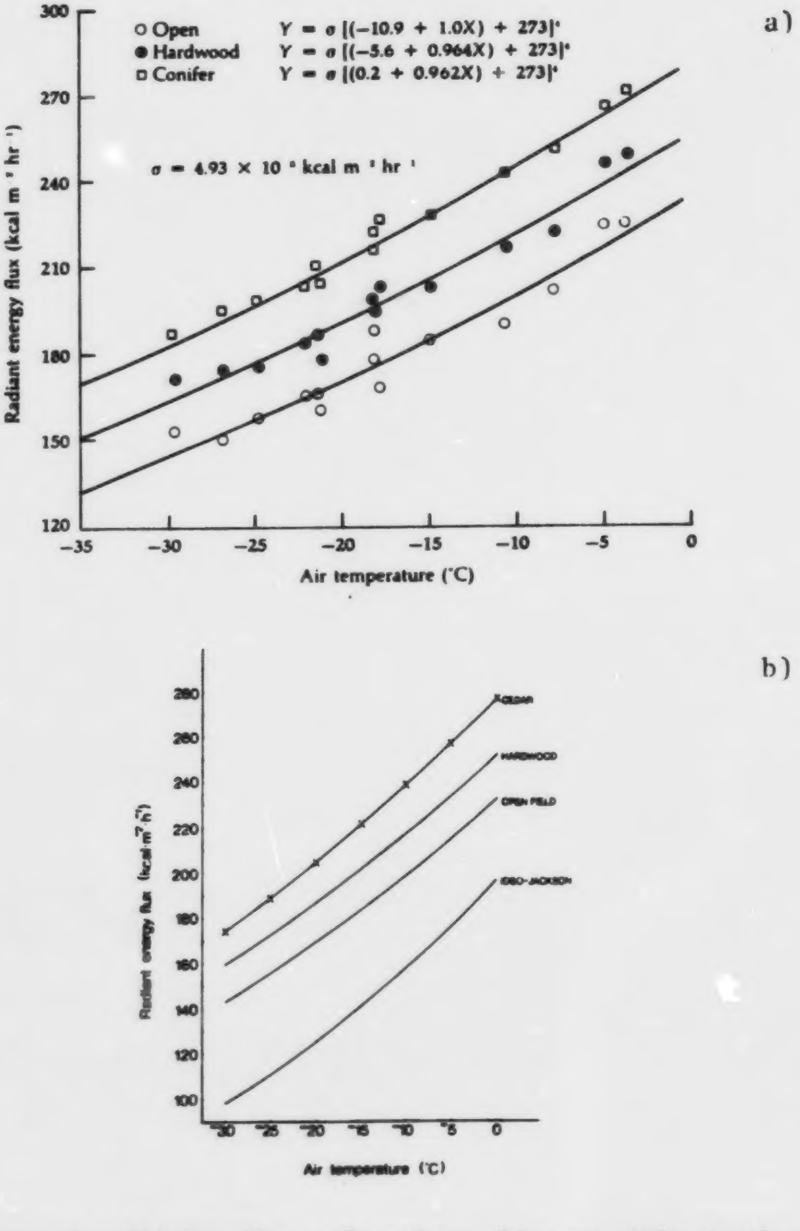


FIGURE 13. Downward radiation flux under clear skies at night in three cover types, Minnesota.
a) Radiation flux under three different cover types (from Moen 1973: 84)
b) Comparison of Moen's equations with the Idso-Jackson equation and the Stephan Boltzmann law using simple assumptions (x). See text for assumptions.

canopies presumeably reflects an unknown difference in canopy closure. The major point in terms of thermal cover is that although a forest floor receives considerably less global radiation by day than does open ground, it gains more longwave radiation at night. The effective longwave emission from ground in a forest at night is less than from open ground (e.g., Perttu 1970).

A portion of the total shortwave radiation is reflected. Albedos, solar reflection coefficients, for various tree species and surfaces are summarized in Table 10 (see also Jarvis et al. 1976:174). All reflectivities are influenced by the amount of vegetative cover, colour of vegetation and soil, and solar elevation angle (Campbell 1977). For example, at a low solar angle the forest has higher albedo; conversely at higher solar angles there is more penetration and absorption increases. Overcast skies reduce the influence of solar angle on albedo.

Another portion of shortwave radiation is absorbed by the canopy before it reaches the forest floor. The proportions of total incoming solar radiation reaching the forest floor vary considerably, as a function of canopy closure, but are commonly less than 15% except in more open pine and larch stands (Table 11). Monsi and Saeki (1953) suggested that a relationship analogous to Beer's law existed between the vertical extinction of light and cumulative leaf area index. This relationship can be expressed:

TABLE 10. Albedo of different surfaces and forest stands

Species	Albedo	Source
Douglas-fir	0.08 - 0.14	Reifsnyder 1967
Pine spp.	0.08 - 0.14	Monteith 1976
Pine spp.	0.11	Reifsnyder 1967
Pine spp.	0.12	Stanhill et al. 1966
Sitka spruce	0.15	Monteith 1976
Sitka spruce	0.16	Landsberg et al. 1973
Deciduous	0.15 - 0.20	Reifsnyder et al. 1971
Deciduous	0.06 - 0.13	Kung et al. 1964
Deciduous	0.18	Budyko 1958
Coniferous	0.10 - 0.15	Reifsnyder et al. 1971
Coniferous	0.12 - 0.14	Kung et al. 1964
Coniferous	0.14	Budyko 1958
Coniferous	0.16	Campbell 1977
Grass	0.24	Campbell 1977
Matted grass (dry)	0.32	Lowry 1969
Matted grass (wet)	0.20	Lowry 1969
Dry soil (light colour)	0.32	Campbell 1977
Fresh snow	0.80	Lowry 1969

TABLE 11. Solar radiation reaching the forest floor as a percent of incoming total shortwave and diffuse shortwave radiation at the top of the canopy or in the open

Stand type	Radiation (% of incoming) Total	 Diffuse	Source
Picea abies (annual average)	2.2		Mayer 1981*b*
P. abies (April-October)			
1700 stems·ha^{-1}	2.4		Vézina 1961
1124 stems·ha^{-1}	2.6		Vézina 1961
815 stems·ha^{-1}	7.3		Vézina 1961
P. abies (mature)			
spring	4.0		Nägeli 1940[a]
autumn	8.0		Nägeli 1940[a]
P. abies (dense, young)	4.5		Knuchel 1941[a]
Abies firma	1.7-8		Monsi and Saeki 1953
A. balsamea (summer and winter, 43 years old)	5.9	7.6	Vézina and Péch 1964
'Mixed mountain forest'[b]	7.3		Mayer 1981[a]
Douglas-fir plantation (21 years old)	7.4	31	Hardy 1975
Mixed hardwoods (August)	9		Reifsnyder *et al*. 1971
Chamaecyparis obtusa	5-15		
Pinus resinosa (winter, 24 years old)	6.6	10.2	Vézina and Péch 1964
P. silvestris (plantations)			
15 years old		8.7	Anderson 1970
30 years old		12.7	Anderson 1970
38 years old		16.4	Anderson 1970
P. silvestris (native, mixed age)		36.2	Anderson 1970
P. radiata (plantations)			
16 years old		14.8	Anderson 1970
30 years old		21.3	Anderson 1970
P. taeda	18	53	Gay *et al*. 1971
P. taeda	32		Gay and Knoerr 1970
P. resinosa (September)	30		Reifsnyder *et al*. 1971
P. densiflora	28-37		Monsi and Saeki 1953
Larix leptolepsis	13-25		Monsi and Saeki 1953
Pine and spruce	27		Perttu 1970
Pine and spruce	35	46	Perttu *et al*. 1980

[a] Visible spectrum only.
[b] Spruce, fir, and beech.

$$I(z) = I(o)\exp{-kL(z)} \qquad (25)$$

where the average irradiance I(z) at any level z in the canopy is related to the irradiance above the canopy, I(o), an extinction coefficient, k, and the leaf area index, L(z), cumulated from the top of the canopy down to level z. Jarvis et al. (1976) modified this relationship to account for the varying path length of solar radiation through the canopy:

$$I(z) = I(o)\exp(-kL(z)\cdot(\operatorname{cosec}\beta - 1)) \qquad (26)$$

where β is the solar elevation angle. Because of difficulties in sampling leaf area index and mean irradiance, few extinction coefficients have been reported for forests. For temperate coniferous stands they center around 0.4 to 0.6 for visible and short wave radiation (Jarvis et al. 1976; Table 2). Assuming a leaf area index of 5.5 the average extinction coefficient for Douglas-fir was 0.5 (Hardy 1975). Equation 25 also works well for net radiation (Landsberg et al. 1973; Spittlehouse and Black 1981), and has a sound theoretical basis.

There are four reasons for adopting an approach different from Eqs. 25 and 26. First, LAI is rarely measured and would have to be estimated by regression (e.g., Gholz et al. 1976, Waring et al. 1978). Second, total projected LAI, which is that estimated by regression, shows no consistent relationship with extinction coefficient k (data collated by Jarvis et al. 1976).

Third, the cumulative pattern of LAI (Eqs. 25 and 26) is unnecessary when the proportion of radiation penetrating the entire canopy is the variable of interest (e.g., Reifsnyder *et al*. 1971). Fourth, it is likely that other variables which are closely related to LAI will probvide a more direct estimate. The most useful relationships for predicting total radiation at the forest floor should have the form:

$$\ln(I/Io) = k(S) \tag{27}$$

or $$I/Io = \exp(-kS) \tag{28}$$

where S is some surrogate for LAI such as basal area or stem density index. The extinction coefficient is then a function of some easily obtainable stand measurement, S:

$$k = \ln(I/Io)/S \tag{29}$$

This approach is simpler than that suggested by Lindroth and Perttu (1981), and preliminary calculations suggest that it has merit (D.J. Vales, pers. comm.).

Along with reducing the total solar radiation reaching an animal, forest canopies alter the proportion of direct and diffuse shortwave. On clear days in the open an animal will always receive both direct and diffuse shortwave; under a canopy it will receive direct radiation only in sunflecks. On clear days diffused light usually represents 10 to 15% of the light at the top of the canopy (Gay et al. 1971; Hardy 1975; Perttu et al. 1980). This percentage increases with increasing cloudiness. As light passes through the canopy the total amount decreases but the diffuse fraction increases. Ratios of diffuse to total shortwave radiation in a 7-10 m tall Douglas-fir plantation (Hardy 1975) were: 11% at 10 m, 36% at 5 m, and 47% at 1 m. Similar proportions of diffused light in radiation transmitted to the forest floor have been documented in other stands: (Berger 1953; Czarnowski and Slomka 1959; Waggoner et al. 1959; Gay et al. 1971). Examples of budgets above and below the canopy are given in Table 12.

The differential transmission of direct and diffuse shortwave has broad implications to the radiation regime expected in coastal forests. Because southwestern British Columbia experiences frequent cloud cover, total radiation will often be less than the potential for a given latitude but diffuse radiation will comprise a large fraction of total radiation. The proportion of total sky radiation transmitted to the forest floor is generally greater on cloudy days when more of the shortwave radiation is diffuse (Brecheen 1951; Ovington and Madgwick 1955; Miller 1959). The increase in shortwave transmission through a canopy on overcast days ranges from 12 to 38% and decreases with increasing crown closure (Table 13). Despite this increase in the fraction of incoming solar radiation transmitted, the amount of radiation reaching the

TABLE 12. Total radiation budget under hardwood and red pine canopies (from Reifsnyder _et_ _al_. 1971: 31)

	Hardwood	Red pine
Extinction coefficient k	−0.89	−0.40
Solar altitude at noon *a* (degrees)	66	51
Radiation above canopy[a]		
diffuse	338	324
direct beam	872	688
total	1210	1012
Radiation below canopy[a]		
total indirect	34	97
penetrating direct	24	160
reflected direct	55	43
total	113	300
Below/above ratios		
Penetrating direct + reflected direct/ direct beam	0.09	0.30
Penetrating direct/ direct beam	0.03	0.23
Total below canopy/ Total above canopy	0.09	0.30
Penetrating direct/ Total below canopy	0.21	0.53

[a] Radiation in mly/min is average for 2-h period centered on local noon.

TABLE 13. Percent of incoming solar radiation reaching the forest floor as a function of cloudiness and crown closure in stands of balsam fir (data of Vezina and Pech 1964: 447) and in stands of spruce, fir and beech (data of Mayer 1981*a*: 290)[a]

Crown closure (%)[b]	Degree of cloud cover[c] Clear	Moderate	Overcast	% increase (overcast over clear)
Abies balsamea				
71	5.9	6.4	7.2	22.4
66	8.0	8.3	10.3	28.8
61	8.7	9.8	11.7	34.5
Picea, *Abies* and *Fagus*				
70	14.2		15.9	12.0
60	19.6		26.5	35.2
50	27.4		37.8	38.0

---

[a] Derived from regressions.

[b] As measured by moosehorn (Robinson 1947) for *Abies* stands; method unknown for mixed stands.

[c] Clear, moderate, and overcast represent <20%, 30-70%, and >80% cloud cover, respectively.

forest floor on an overcast day is much less (95 versus 687 J·cm^{-2} at 50% crown closure; regressions of Mayer 1981a: 290).

Although the best approach to predicting radiation at the forest floor would utilize leaf area index, that value is seldom measured. Potential surrogates include any stand measurement that reflects the opacity of the crown to light. Because diameter is closely related to LAI, indices employing diameter are likely to be reliable predictors. Summation of diameters per unit area or stem density index (Wellner 1948; Miller 1959; Vézina 1965) and basal area (Kittredge 1948; Wellner 1948; Vézina 1965) have been examined relative to light intensity below the canopy (Table 14, Figs. 14 and 15). These variables were about equally good as predictors of light penetration in pine types (Wellner 1948; Fig. 15). Percent of light penetrating declined to about 40% at basal areas of 200 ft^2/acre (46m^2·ha^{-1}) for small-crowned species such as pine and 15% for large-crowned species such as western hemlock. In long-crowned species (e.g., *Abies balsamea*) the stem density index predicted light transmission better than did basal area (Vézina 1965). In these latter stands only 8% of the incoming light was transmitted at a basal area of 46 m^2·ha^{-1}. Apparently anomalous low values of radiation below a pine stand of small basal area (30-year-old stand, Table 14) resulted from a greater amount of foliage in the younger stand (Kittredge 1948). These observations indicate that both closure and thickness or depth of the crown influence light penetration. That effect is

TABLE 14. Percent of total radiation reaching the forest floor in eastern white pine stands of different ages and basal area (Kittredge 1948: 49)

Basal area (m^2/ha)	0	25.2	29.1	35.6	72.5
Age (years)	-	30	50	55	uneven
Radiation at ground (%)	100	6	22	14	6

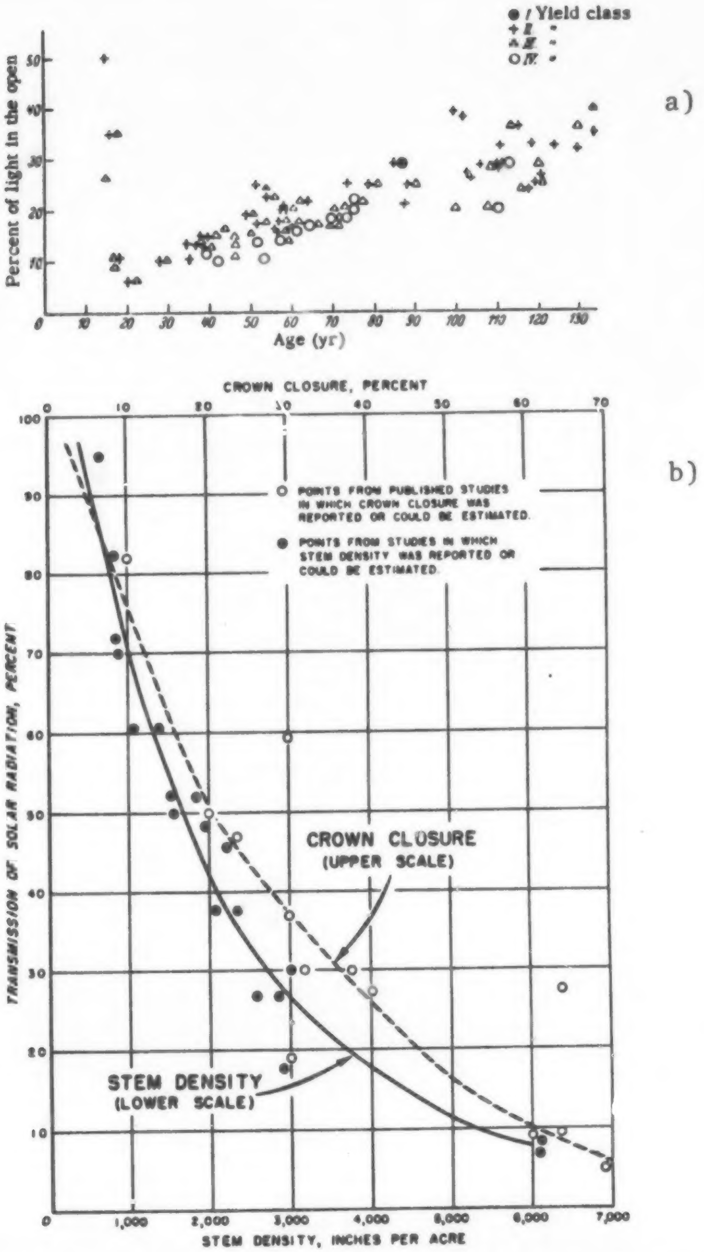


FIGURE 14. Transmission of total solar radiation to the forest floor as a function of stand attributes.
a) Percent of light reaching the forest floor as a function of age in a true fir stand (from Geiger 1966: 301).
b) Percent of solar radiation reaching the forest floor as a function of stem density and crown closure in pine stands. 1000 inches/acre = 62.7 m/ha (data of Miller 1959 as presented by Reifsnyder and Lull 1965: 74).

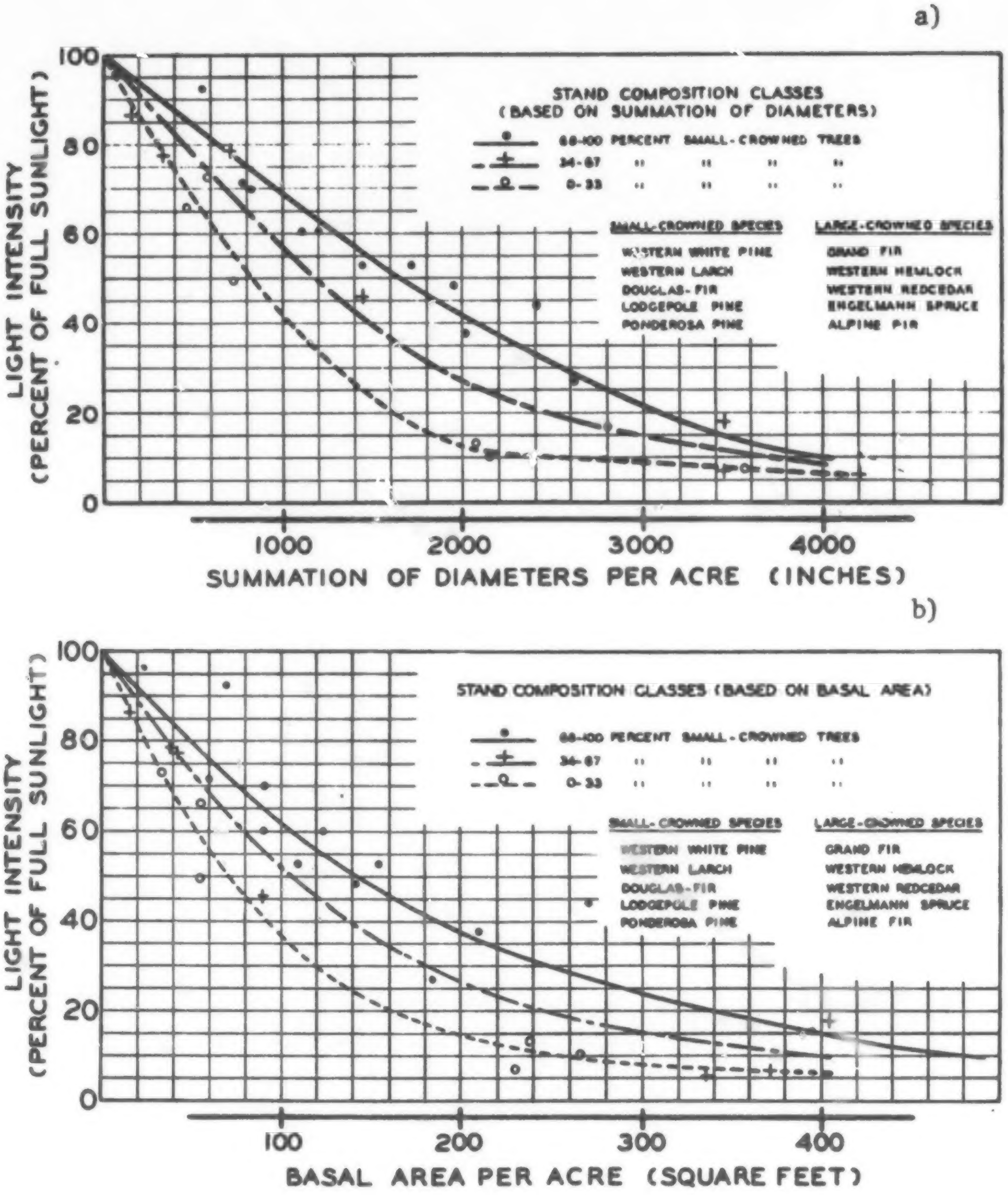


FIGURE 15. Light intensity beneath the canopy in mature stands of the western white pine type as a function of stand composition class and:
a) Summation of diameters per acre (1000 inches/acre = 62.7 m/ha), or
b) Basal area (from Wellner 1948: 17).

expected given that it is the downward cumulative leaf area index, L(z), that is related to light extinction. Note that the relationships of Figures 14 and 15 follow the form of Eq. 28.

The influence of canopy depth reduces the utility of crown closure as a measure of radiation transmission once crown depth increases or the canopy becomes dense (Berger 1953; Miller 1959). Some early observations on light transmission were made for the purpose of obtaining a measure of crown closure, assuming percent transmission and percent crown closure summed to 100 (e.g., Wright 1943). In fact, these two values rarely sum to more than 80% (Miller 1959; Vézina and Péch 1964), indicating the role of solar angle and crown depth in reducing light penetration. Despite these limitations, relationships between crown closure and light penetration have been documented (Table 13, Fig. 14b). For a mixed spruce, fir, and beech forest Mayer (1981a) obtained:

$$\text{Sunny days:} \quad SW = 2561.8 - 52.5C + 0.3C^2 \quad (r^2 = 0.96) \tag{30}$$

$$\text{Overcast days:} \quad SW = 254.2 - 3.5C + 0.0062C^2 \quad (r^2 = 0.50) \tag{31}$$

where SW = total or global shortwave ($J \cdot cm^{-2}$) and C = crown closure (%). The approach of Vézina and Péch (1964:446) is more readily generalized, but their equations are in error. Altering their equations to fit their data produces:

Jack pine $Y=98.758(9.7792)^{-X}$ (32)

Balsam fir $Y=100.17(9.6234)^{-X}$ (33)

where Y is the radiation under a canopy as a percent of that in the open and X is crown closure as a proportion, 0-1.0.

Simpler relationships may also prove adequate. Roussel (1962) related relative illumination (Er) to the number of trees per ha(N):

$$Er = k/k+N \tag{34}$$

where k is about 20 for spruce. From Roussel's relationship the relative illumination below a canopy would decrease rapidly with increasing stem density. The rapid decline in below-canopy light with increasing stem density, stem density index, basal area, or crown closure is consistent among species (Table 11, Figs. 14b and 15) and produces age-related effects (Fig 14a; data of Anderson 1970 in Table 11).

Efforts to extract a detailed, daily energy budget of an animal would have to acknowledge diurnal changes in solar radiation. Diurnal variations in solar radiation under a canopy have been documented in coniferous and hardwood stands (Fig. 16). Direct beam levels differed markedly over a 12-h period between a red pine stand and a hardwood canopy (Fig. 16a). Time of maximum solar radiation measured in a Scotch pine stand also varied with height of measurement and

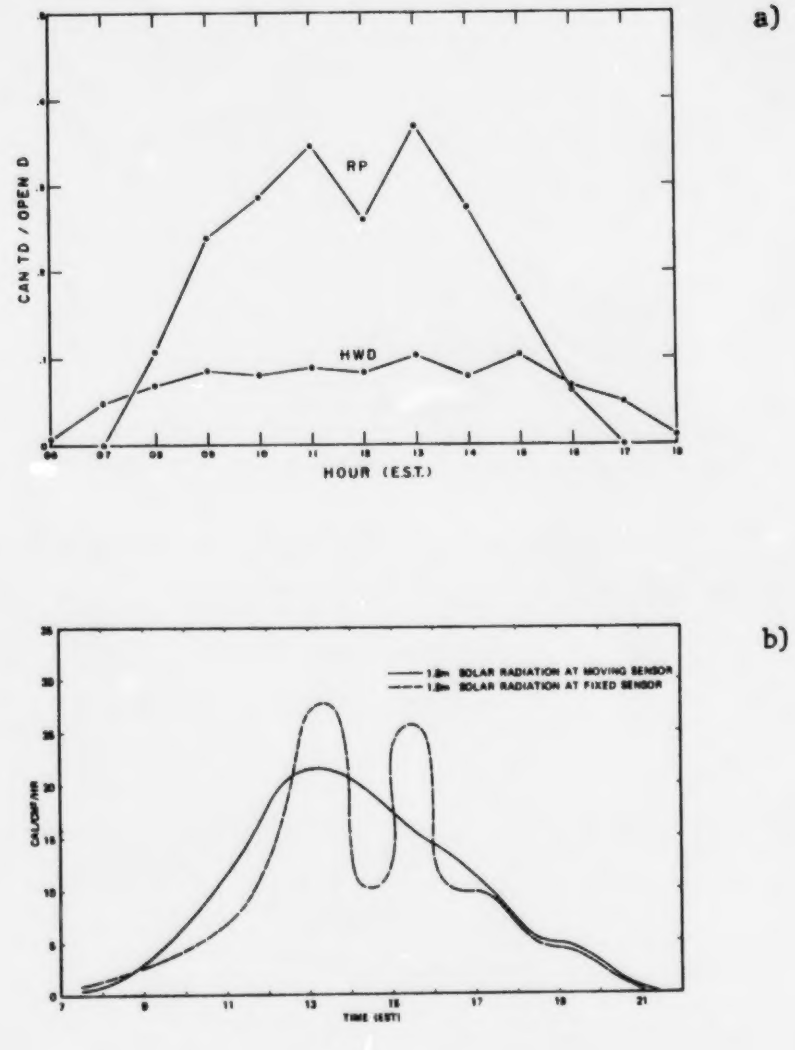


FIGURE 16. Diurnal patterns in solar radiation reaching the forest floor. a) Ratio of total direct beam radiation appearing under the canopy (CAN TD) to direct beam radiation appearing above the canopy (OPEN D). RP = red pine; HWD = hardwood canopy (from Reifsnyder et al. 1971: 30).
b) Diurnal variation of solar radiation below a Scotch pine canopy in June for fixed and moving sensors at 1.8 m (from Mukammal 1971: 33).

season (Fig. 16b). The maximum level of solar radiation at 10 m occurred 100 minutes later than that at 1.8 m in June, 40 minutes later in July, and at the same time in September. In early morning and evening most of the solar radiation reaching the ground below a red pine canopy was reflected and diffuse light (Waggoner et al. 1959). Shortly before and after solar noon, a greater portion was from direct radiation.

Total or allwave radiation, measured using net radiometers, incorporates effects of both longwave and shortwave radiation. Within a stand, net radiant energy is available for transformation to other forms of energy (e.g., latent or sensible heat). In an 85-year-old spruce stand, this gain in energy (as a percent of net allwave radiation at the top of the canopy) represented 6.7% at the forest floor and 22.3% within the canopy (Mayer 1981b). Although much of this energy is used in transpiration, a large portion of the remainder appears as heat within the canopy, and forest floors are relatively cool during summer (see temperature profiles of Section 3.2.2).

In summary, forest canopies influence both longwave and shortwave irradiances beneath them. Longwave irradiance can be predicted by the Stephan Boltzmann law assuming an emissivity of 1.0 and canopy temperature about 1°C above air temperature. Downward irradiance decreases with canopy closure (Fig. 13) probably in a curvilinear fashion. Amounts of shortwave irradiance decrease as a function of downward cumulative LAI; this relationship is naturally a function of canopy depth but can be approximated by crown closure, stem density index, or basal area (Figs. 14 and 15). The proportion of diffuse radiation below the canopy will be greater than in the open (Tables 11 and 12).

3.3 Effects of Forestry Practices

Vegetative structure influences the major abiotic components contributing to Te (Section 3.2). Because forestry practices influence vegetative structure, these practices determine the utility of any stand as thermal cover. The effects on thermal cover are mediated primarily through changes in height, length, and closure of crowns. Thus, forestry practices such as thinning, fertilization, or pruning which change these crown attributes will modify the stand's ability to provide thermal cover. The impact of forestry practices are treated separately for each abiotic component of Te.

3.3.1 Throughfall And Interception of Rain

Throughfall increases with reduced density of the residual stand although not in direct proportion to that reduction (Table 15). Overall results from Leyton _et_ _al_. (1967) for a 23-year-old Norway spruce plantation indicate an increase of about 10% in throughfall with thinning, which is substantially less than the percentage reduction in basal area (approximately 29%). Similar increases in throughfall of 13 to 14% with a reduction in basal area of 51% were reported by Goodell (1952) for thinned

TABLE 15. Relationship between throughfall of rainfall and measurements of stand density in lodgepole pine (modified from Kittredge 1948: 109)[a]

	Throughfall for a rainfall of 25 mm (%)				
	77	85	88	90	97
Trees(per ha)	944	551	509	447	363
Basal area($m^2 \cdot ha^{-1}$)	36.5	22.0	15.1	14.9	9.2
Stand density index	310	188	134	134	86

[a] Modified from interception values derived by Kittredge from regression equations of Niederhof and Wilm (1943) in Table 2.

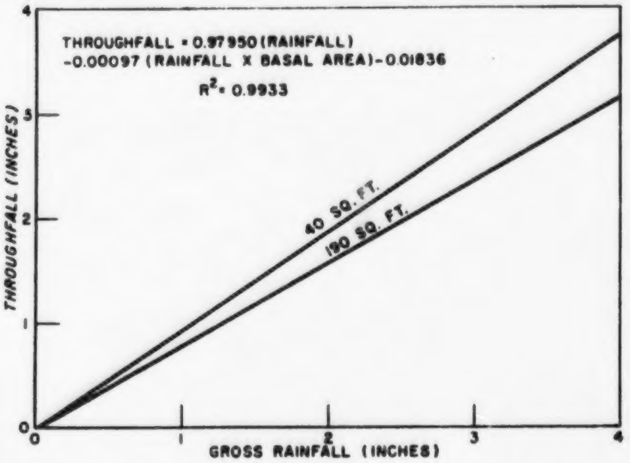


FIGURE 17. Relationship of throughfall with rainfall for basal areas of 40 and 190 ft^2/acre (9.2 and 43.6 $m^2 \cdot ha^{-1}$) in loblolly pine (from Rogerson 1967: 190).

lodgepole pine stands. He also reported a 15 to 21% increase in throughfall when basal area was reduced 60% by removing 84% of the stems/acre.

Both Delfs (1967) and Spittlehouse and Black (1981) observed modest reductions in throughfall with light thinning. Their findings are partially explained by analyses of Niederhof and Wilm (1943; see Table 2) and of Rogerson (1967) that indicate the influence of thinning will be much more pronounced in larger storms (Fig. 17). Expressing the relationship of Rogerson (Fig. 17) for the extremes of basal area he studied yields:

$$40\ \mathrm{ft}^2\ \mathrm{BA}: \quad T = 0.941P - 0.018 \tag{35}$$

$(9.2\ \mathrm{m}^2 \cdot \mathrm{ha}^{-1})$

$$190\ \mathrm{ft}^2\ \mathrm{BA}: \quad T = 0.795P - 0.018 \tag{36}$$

$(43.6\ \mathrm{m}^2 \cdot \mathrm{ha}^{-1})$

If the relationships of Niederhof and Wilm (1943) or Rogerson (1967) are general, thinning will have a greater influence on throughfall and the potential of a stand to reduce wetting in winter than in summer.

One silvicultural treatment considered among potential techniques to create deer winter range in managed stands is the creation of small openings during thinning to favour browse production. Several workers have commented on the influence of opening size on net rainfall. Delfs (1967) suggested that openings in Norway spruce must be at least 2 tree heights in diameter before all rainfall reaches the ground. In lodgepole pine, Niederhof and Wilm (1943) obtained the relationship:

$$T - 0.766P + 0.102R - 0.423 \qquad (37)$$
$$(r^2 = 0.75)$$

where T and P are in inches and R is the radius of the opening in feet. From this relationship throughfall should increase about 8.5mm for each m increase in opening radius. For radii exceeding about 5.5 m (about 1 tree height in diameter), net rainfall should approximate gross rainfall in the open. Sparse data of Geiger (1966:352) indicate similar results: throughfall of 87% P at a diameter of 12 m or 0.46 tree height; about 100% P at 1 tree height diameter (25.8 m).

The effect of pruning differs from that of thinning, presumably because it involves a lesser reduction in the canopy's storage capacity. Whereas effects of thinning become more pronounced at greater storm sizes (Fig. 17), effects of pruning are significant only at storms less than 4 mm (Table 16). The largest difference occurs in storms less than 1.1 mm, or below the canopy saturation value of most conifer canopies, where a reduction in canopy storage has the most influence (e.g., Fig. 4). Stemflow is reduced by pruning (Thorud 1963).

Because canopies seldom intercept more than 10 to 20% of

TABLE 16. Influences of pruning on throughfall and stemflow during storms of different sizes in red pine (Pinus resinosa) (modified from Thorud 1963: 454)

	Storm size (mm)				
	0-0.25	0.26-1.0	1.1-4.0	4.1-19.5	19.5+
Throughfall (%)					
Unpruned	15.3	26.3	41.0	73.6	82.4
Pruned	52.5	72.4	72.6	80.3	82.6
Change with pruning	+37.2	+46.1	+31.6	+6.7	+0.2
Stemflow (%)					
Unpruned	0.0	0.0	0.1	1.8	3.3
Pruned	0.0	0.0	0.1	0.9	1.8
Change with pruning	0.0	0.0	0.0	-0.9	-1.5

TABLE 17. Air temperature in canopy (5.5 m) compared with temperature near ground (20 cm) in thinned and unthinned white pine and Scotch pine stands during July to September (data of Kittredge 1948: 55)

	Temperature in canopy	
Stand	Unthinned	Thinned
White pine	warmer by 1.8%	cooler by 9.2%
Scotch pine		cooler by 14%

the gross precipitation in larger storms (Fig. 4), changes in forest structure have to be large before seasonal throughfall is altered by more than 10% (e.g., Table 15, Fig. 17). Effects of pruning will appear in smaller storms; effects of thinning will appear in larger storms provided sufficient basal area is removed. Openings to create forage would have to be 1 to 2 tree heights in diameter before throughfall would approximate 100%. Potential influences on throughfall resulting from silvicultural practices in younger stands could be estimated from changes in crown closure or basal area. Available data (e.g., Niederhof and Wilm 1943; Thorud 1963; Rogerson 1967; Giles 1983) suggest that effects of silvicultural practices will be most apparent in coefficient b of the relationship $T = bP-a$.

3.3.2 Temperature

Kittredge (1948) reported differences in air temperature between 8 inches (20 cm) and 18 feet (5.5 m) above the ground in thinned and unthinned white pine and Scotch pine stands (Table 17). In both stands the thinned portions had warmer temperatures near the ground than in the canopy whereas the unthinned portions had warmer temperatures in the canopy than near the ground (also see Fig. 7). These observations suggest that light thinning would create a more favourable thermal environment for deer or elk during cold, daytime conditions, but less favourable during hot, dry daytime and cold, wet nighttime conditions.

For small openings (12-87 m in diameter) in a stand 26-m tall, data of Geiger (1966:354) indicate a reduction in nighttime minimum temperatures of about 0.1 to 0.2°C for each meter increase in radius; daytime maximum temperatures increased about 0.1°C for each meter increase in radius.

Partial cuttings produce effects on air temperatures intermediate between those of open areas and uncut forest. Generally, the lighter the cutting the more the temperatures resemble the uncut forest and vice versa. Figure 18 illustrates temperature profiles for unlogged, partially logged, and clearcut, mixed conifer forests in Oregon.

3.3.3 Wind

Although there appear to be no studies specifically documenting effects of silvicultural practices on windspeed, the relationships in Section 3.2.3 allow prediction of probable effects. Provided trees are not strongly self-pruning and canopies have not lifted well above the ground, increased height of a stand reduces windspeed at the level of deer or elk (Fig. 10). Heavy thinning would likely increase turbulence and, by encouraging understory growth, would serve to decrease horizontal windspeeds near the forest floor (Fig. 8b, 8c, and 9c). Pruning would increase wind speed to the detriment of a favourable Te for thermoregulation during winter, but in combination with effects on radiation might produce favourable thermal cover during hot summer conditions (Fig. 8b). Thinning

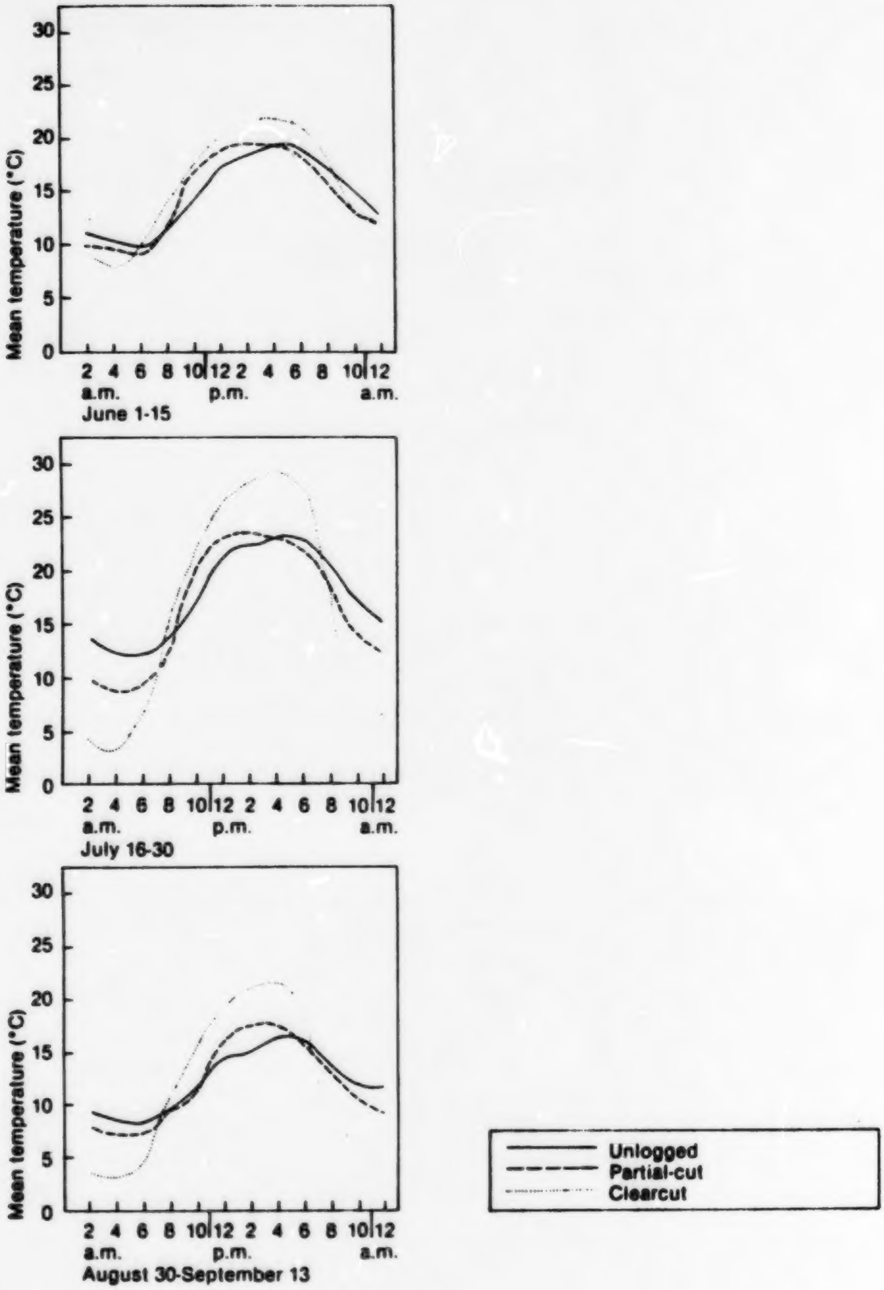


FIGURE 18. Diel patterns in air temperature for unlogged, partial-cut, and clearcut mixed forests in northeastern Oregon (from Thomas *et al.* 1979: 113).

would have little effect unless it encouraged understory production which would decrease wind speed. Any treatment that encouraged vegetation within the first 2 m of the ground would effectively decrease the wind velocity experienced by deer or elk.

3.3.4 Radiation

The relationships between light penetration and basal area or stem density (Figs. 14 and 15), indicate that any forestry practice reducing the latter two variables will increase shortwave radiation at the forest floor. Downward longwave radiation will be decreased (Fig. 13).

Thinning a conifer stand increases light intensity at a rate greater than the rate of removal of trees or basal area (Reifsnyder and Lull 1965; Table 11). Removal of 17 to 24% of basal area increased total illumination 2.9 to 4.6 times; this effect was largely lost by 7 years after thinning (Savina 1956, Table 18). Similarly, reductions in basal area of balsam fir stands of 12% and 36% increased below-canopy radiation intensity by 25% and 50%, respectively (Vézina 1965). Broadly, a decrease in crown closure of 10% increases radiation intensity under the canopy by 30 to 40% on clear days and 35 to 65% on overcast days (Table 13). The effect of a unit reduction in crown closure on below-canopy radiation is non-linear, and much greater at lower crown closures (presumably because lower crown closures have less overlap and removal of one unit of cover is more likely to

TABLE 18. Illumination below the canopy of a stand before and after thinning (data of Savina 1956 from Reifsnyder and Lull 1965: 75)

	Illumination as compared with unthinned area A taken as 100	
Time of observation	area B[a]	area C[b]
1939: Before thinning	90	120
After thinning	290	460
1940: 1 year after thinning	170	230
1946: 7 years after thinning	105	125

[a] 21% of trees removed (17% of basal area)

[b] 27% of trees removed (24% of basal area)

create an unimpeded path for light).

The initial increase in radiation reaching the forest floor after thinning is reduced by subsequent growth in crown width (or crown closure; Fig. 14b) and crown height, which increases the cumulative leaf area index. During periods of positive net radiation flux (and ignoring influences of wind speed), thinning or spacing would have the effect of increasing operative temperatures. During winter nights such practices would reduce operative temperatures by reducing longwave irradiance down from the canopy (e.g., Fig. 13a).

The effect of small openings also would be to decrease downward irradiance at night and effectively increase outgoing radiation from the clearing. Data of Geiger (1966:353) indicate that outgoing radiation as a percent of that in open land increased approximately linearly from 11 to 66% in openings 12 to 47 m in diameter (about 0.5 to 2 tree heights).

Slashburning is likely to alter the albedo of soil surfaces so that a smaller proportion of the total shortwave irradiance is reflected than in unburned open areas. Burning, however, also affects soil thermal properties so that slashburning effects on net radiation are unclear. Furthermore, natural succession on Vancouver Island would generally permit only a short-lived change in albedo.

3.3.5 Operative Temperature

The broad effects of forest cover on an animal's thermal environment are generally favourable, and even understory sufficiently dense can meliorate moderate thermal stress (Fig. 19). The effect of a specific forestry practice is usually less clear.

The influence of forestry practices on operative temperature results from their influence on the separate but interacting components of operative temperature. Although it is theoretically possible to do so, such influences have never been calculated. In part the difficulty results from the number of factors involved and the complex nature of their interactions (App. 1). The most efficient approach would be to use a simulation model incorporating the relationships in Sections 3.2 and 3.3 to modify processes contributing to Te and re (Eq. 1). Ideally such an approach would be extended to include effects of windspeed.

Crude estimates of the effects individual forest practices have on the thermal environment of an animal can be derived from information in Sections 3.2 and 3.3 (Table 19). That derivation emphasizes the complexity noted. For example, during winter clearcuts and small openings can benefit an animal during day but not during night (Table 19). Similarly, the negative influence associated with thinning effects on windspeed during winter could be offset by an associated increase in understory. The ratings summarized in Table 19 are thus approximate, but do

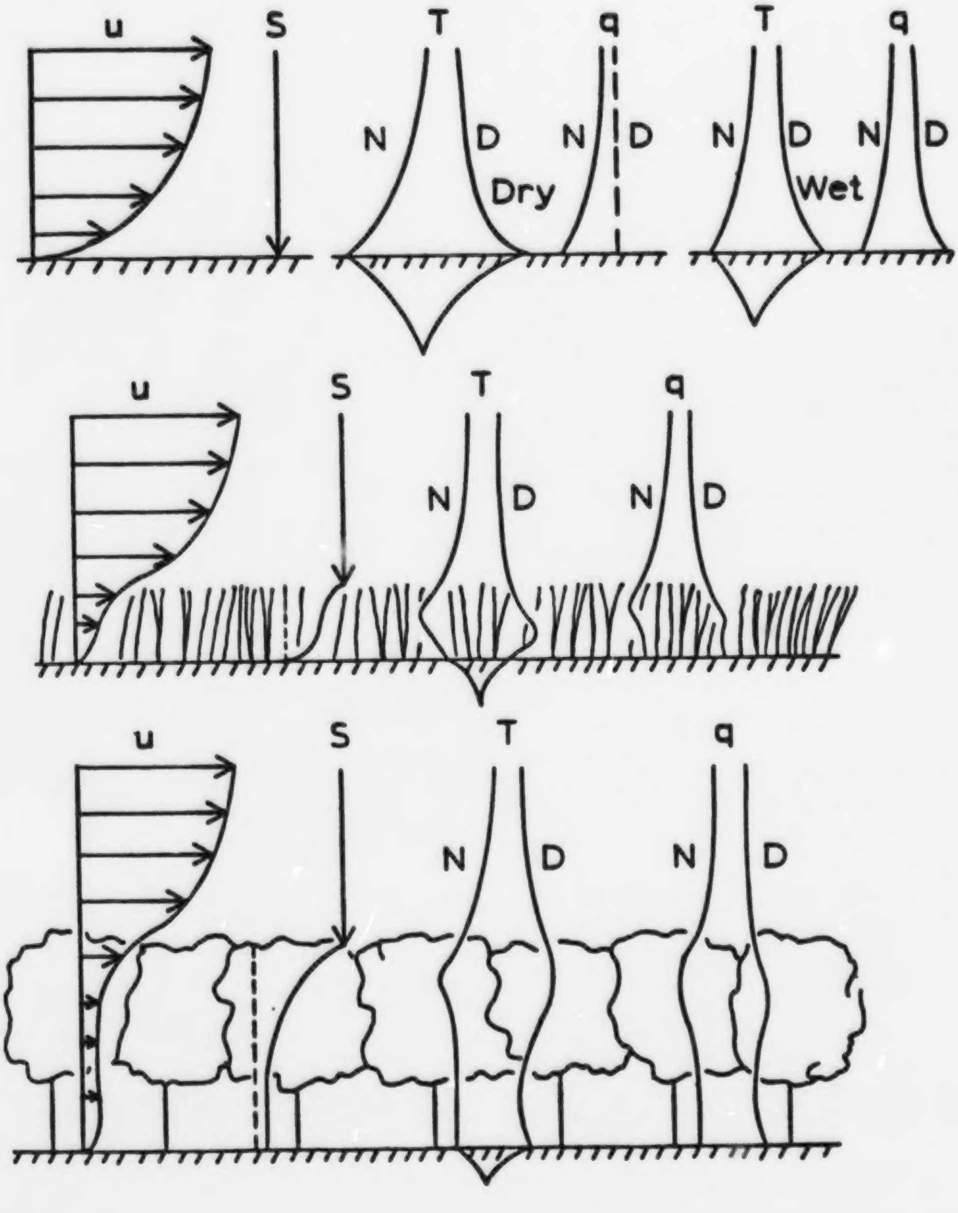


FIGURE 19. Typical profiles of wind speed (u), solar radiation (S), air temperature (T) and air specific humidity (q) for day (D) and night (N) conditions. From top to bottom the cover types are bare ground, dense shrub layer, and deciduous forest.

TABLE 19. Relative influence of forestry practices on operative temperature (Te) and its abiotic components by season

Forestry Practices	Season									
	Winter					Summer				
	Throughfall	Temperature	Wind	Radiation	Te	Throughfall	Temperature	Wind	Radiation	Te
Clearcut	---[a]	--+[b]	---	--+[b]	--[c]	-	--	+	--	-
Spacing	-	0	0	0	0	0	+	+	0	0
Thinning	--	--	-	--	-	-	-	+	-	-
Fertilizing	+	+	+	+	+	+	+	0	+	+
Pruning	-	0	-	0	0	-	+	+	0	+
Small openings	--	-+[b]	0	+	+	-	-	0	-	-
Residual conifer patches	+	++	++	+	++	+	+	-	+	+

[a] Negative influence (-); positive influence (+); no strong influence (0).
[b] - at night; + during day.
[c] Te estimates combined effect on animal's thermal environment.

indicate potential values gained from particular forestry practices.

4 INFORMATION NEEDS AND PRIORITIES

Given the primary objective of the IWIFR program (to determine how intensive forestry practices influence the ability of forested land to support deer and elk), there are some major information needs. This review and analysis suggest that an operational definition of thermal cover is possible. That definition would permit evaluation of a forest stand's ability to meet the apparent thermal needs of deer and elk (Section 4.1). Before the definition can be applied and selected stand structures evaluated, however, specific data must be acquired (Section 4.2).

4.1 Potential Importance of Thermal Cover

Necessary data are lacking to permit an effective evaluation of the potential importance of thermal cover. We can, however, indicate how that evaluation could occur and which specific data should be collected. Sufficient information is available to estimate approximate daily energy costs of black-tailed deer and Roosevelt elk (App. 2 and 3) but these estimates do not incorporate specific activity budgets and use linear rates of weight change (App. 4). From data of Parker and

Robbins (1984) we can derive approximations of metabolic rate at different values of Te (Table 20). Values in the thermoneutral zone were about 90 $kcal \cdot kg^{-0.75} \cdot d^{-1}$ for fed mule deer in winter. These are higher than the interspecific basal metabolic rate (BMR) of 70 $kcal \cdot kg^{0.75} \cdot d^{-1}$ (Kleiber 1947) but include costs of standing and heat of digestion.

Values of energetic costs (App. 2 and 3) are first approximations and allow only crude comparisons. Such comparisons suggest that daily costs of thermoregulation (absence of thermal cover at low windspeeds) for a black-tailed deer at Te $\geq$ 10°C are about 10 to 40 $kcals \cdot kg^{-0.75} \cdot d^{-1}$ (Table 20) which equals or exceeds the requirements for weight recovery after winter (App. 2). Similarly, in the same thermal regime the cost to an adult female would be about 20 to 80% of the cost of producing a single young during summer and fall. At an operative temperature of 0°C in winter, costs of thermoregulation for an elk calf are about 50 $kcal \cdot kg^{-0.75} \cdot d^{-1}$ or 70% of basal metabolic rate (assuming elk exhibit the same costs as deer in the thermoneutral zone).

These simplistic comparisons suggest that thermal cover is important to deer and elk if it can effectively maintain operative temperatures within the thermoneutral zone. The comparisons are unfortunately flawed. First, it is unclear what a cost of 80% of the reproduction of a single fawn or 70% of an elk calf's BMR means in terms of fitness. We know that energy devoted to thermoregulation can not be used for other purposes.

TABLE 20. Approximate metabolic rates of standing, fed mule deer and Rocky Mountain elk (kcal·kg$^{-0.75}$.d^{-1}) as a function of Te[a]

	Mule deer		Elk	
Te (°C)	Fawns	Adults	Calves	Adults
Winter				
-40	202	202	-	-
-30	158	158	94	-
-20	98	98	72	-
-10	91 - 137	91	115	-
0	91 - 137	91	144	-
10	-	118	163	115
20	-	146	-	118
	≥ 1 year		≥ 1 year	
Summer				
0	173		-	
10	101 - 132		118	
20	101 - 130		118 - 173	
30	142 - 158		137 - 170	
40	202 - 218		158 - 166	

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[a] Extrapolated from Parker and Robbins (1984: 1418). Includes the cost of standing and specific dynamic action (heat of digestion).

It is unlikely that the fawn crop would be reduced by 80% or that elk calves would suffer 70% mortality. Appendix 3 presents costs as $kcal \cdot d^{-1}$; knowing the weight of an animal, data of Table 20 could be expressed in the same units. Such conversion would facilitate evaluation of potential tradeoffs. For example, increased costs of thermoregulation might be unimportant if sufficient forage energy were available to meet those costs. The animal's fitness might then be unaffected. Second, the data on thermoregulation are extrapolated from other subspecies. Third, it is not known whether operative temperatures for black-tailed deer and elk are frequently outside their thermoneutral zones in southcoastal British Columbia.

The first fault cannot be corrected readily. It is common to any comparison derived from energetics. The value of the common currency of calories is that consistent relative comparisons are possible. Energy balance is directly related to reproduction and survival, but no absolute relationships with fitness have been established. The last two failings represent information needs. If they were known we could use the relationships of Chapter 3 to evaluate how frequently thermal environments represented an energy cost to the animal and how forestry practices could ameliorate them.

4.2 Information Needs

The definition of thermal cover assumes that the zone of minimum heat production is known. Currently it is not known for either black-tailed deer or Roosevelt elk, although data exist for related subspecies (mule deer and Rocky Mountain elk). Because of their similarity in size, shape, and pelage, relationships may differ little between the two elk subspecies. Relationships for the deer species may differ significantly, primarily as a function of their size. One major information need is a definition of the zone of minimal heat production for black-tailed deer; that is, upper and lower critical temperatures (Fig. 1). For the definition to have utility in the field it should be defined in terms of Te and Tes. Given the frequency of precipitation in southcoastal British Columbia and the importance of wetting to heat loss, the potential influence of wetting also should be evaluated.

While a metabolic measurement of thermoneutrality is critical to an objective ranking of a stand's potential to provide thermal cover, behavioural definitions of thermal cover are also important. Behavioural definitions will be broader and incorporate more variability (Fig. 2), but represent an integration of tradeoffs as perceived by the animal. Because forage production or quality and thermal environments differ between areas, it is important that these apparent tradeoffs be assessed in the area where management will be applied. For example, the definition of thermal cover proposed by Thomas *et* al. (1979) was based on 7 years of observations of radio-collared elk in the proposed management area.

The relationships between forestry practices, forest structure, and the abiotic components of Te are less likely to be as specific as are behavioural and metabolic responses of the animals. Even if no area-specific data were collected to document forest influences on abiotic factors, one important need would remain: a simulation model or other device for relating the interacting components of Te to general changes in forest structure. Ideally, area-specific abiotic data would be collected and used to evaluate the applicability of data reviewed in this analysis to Vancouver Island and the adjacent mainland. The need for such information is more apparent when one considers the sparsity of data for Douglas-fir stands. There are almost no data available for western red cedar or western hemlock stands.

4.3 Links with Other Projects

Two of the specific information needs could be developed without close interaction among IWIFR projects. These needs are: definition of the zone of critical heat production for black-tailed deer and development of a simulation model of the relationships producing Te. Development of model parameters for radiation would profit from close cooperation with the project on salal-overstory relationships (Vales 1984)[2]. Evaluation of the model's utility then would profit from close cooperation with the IWIFR deer and elk projects. Such cooperation would be valuable for two reasons: 1) analysis of the abiotic data would examine the applicability of relationships summarized in this report, particularly as applied to Douglas-fir stands; and 2) comparison of the relative roles of objectively-defined need and behaviour or preference (as these appear in empirical observations of habitat selection) would assist decisions regarding the relative role of thermal cover.

4.4 Priorities

The priority of studying thermal cover relative to other components of deer and elk habitat has been evaluated (Janz *et al*. 1980; Nyberg 1985; McNay and Davies 1985). Those analyses noted a need to clarify concepts of thermal cover. The present analysis has illustrated the reasons why thermal cover has proven to be an elusive concept and difficult to rank. This analysis assigns research priorities based on actions needed to clarify concepts of thermal cover and to evaluate whether or not and how these concepts should be incorporated into considerations of forestry practices in southcoastal British

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[2] Vales, D.J. 1984. Functional relationships between salal understory and forest overstory. Unpubl. M.Sc. proposal, Faculty of Forestry, University of British Columbia, Vancouver. 53 pp.

Columbia.

4.4.1 Priority One: Zone of Minimum Heat Production

It is impossible to evaluate potential need for thermal cover without an objectively-defined measurement of costs for thermoregulation (e.g., Fig. 1). The measurement should be metabolically based to reduce ambiguity and should document lower and upper critical temperatures. Before it could be used as a management tool the definition would have to incorporate production targets. For application in the relatively moist areas of Vancouver Island and the adjacent mainland it should incorporate effects of high humidity or wetting. To be of utility in field application the measurement should be designed in terms of operative temperature incorporating the interacting effects of abiotic variables (e.g., Te or Tes). Its utility will be increased if it acknowledges the different energy requirements of resting (survival), maintenance, and production.

These major criteria can be met by experiments using a metabolic chamber designed to control specific abiotic variables. Specific details of experimentation with black-tailed deer are discussed by Parker (1986).

4.4.2 Priority Two: Computation of Te

Part of the confusion surrounding the concept of thermal cover derives from the fact that the operative temperature experienced by an animal is a product of many environmental variables (Section 3.1.1). Attempts to relate thermal cover to single abiotic variables have either failed or revealed great variability, other than at extremes. Even knowing the zone of minimum heat production (priority one), it would be impossible to assess the metabolic needs for thermal cover in a specific environment without some efficient way of calculating Te and re. Ideally the approach should incorporate effects of changing forest structure on the resultant Te and re. That approach would permit evaluation of impacts of particular forestry practices on the energetic cost of thermoregulation borne by the animal. Given the complexity of the interactions (Section 3), simulation modeling seems to be the appropriate vehicle. The analysis (Sections 3.2 and 3.3) suggests that many of the impacts of forest practices can be indexed by two or three variables: height of the stand, basal area, and crown volume or closure (MCC of Bunnell _et_ _al_. 1985).

An appropriate model would attain three ends: 1) it would document the potential magnitude of thermal stress of deer and elk in southcoastal British Columbia; 2) it would permit evaluation of the impacts of particular forest structures and forestry practices on that stress; and 3) it could be used to generate simpler relationships between easily measured forest variables and thermal stress based on complex underlying relationships.

There is a logical order in attaining priority two (computation of Te):

1. Develop a simulation model capable of calculating Te for a variety of abiotic and stand conditions. That model would require data from priority one and could be developed most efficiently at the University of British Columbia. For abiotic and forest relationships it would rely initially on data from literature.
2. Use abiotic data from selected weather stations or collected by other IWIFR projects to evaluate applicability of the general relationships incorporated in the model to conditions on Vancouver Island. The model could be refined to address the magnitude of thermal stress on Vancouver Island in different stand conditions. This step involves cooperation with the other three major components of the IWIFR program (deer, elk, and habitat).
3. Develop simple graphical displays of the relationships between one or two simple forest variables and the magnitude of thermal stress for conditions specific to Vancouver Island.
4. Use the model to compare metabolically defined need for thermal cover with actual use of thermal cover (priority three). The need should be evaluated for three levels of energy requirements: resting (survival), maintenance, and

production.

5. If desirable, incorporate a simplified version of the model to explore tradeoffs with other energetic costs or inputs borne or received by the animal (e.g., locomotion in snow, forage production). This last step would be slow in developing, would require cooperation among all IWIFR projects, but would assist the activities proposed for Phase 2 of the IWIFR program.

4.4.3 Priority Three: Preference for Thermal Cover

For many reasons an animal's preference for cover probably can differ from its metabolic need for cover (Section 3.1.3, Fig. 2). The empirical preference may result from traditional movement patterns, density of predators, or tradeoffs with other metabolic needs. It is therefore important to document preference within the area of interest; extrapolation of results from other areas is unlikely to be helpful. Without some ojectively defined measurement of thermal cover (priorities one and two), it is unclear whether an animal's use of cover is in response to need or preference. However, the use of cover through preference rather than metabolic need has clear management implications. It indicates the animal's ranking system under specific environmental conditions. Because we have no unequivocal way of comparing energetic tradeoffs as perceived by the animal (Section 4.1), observed preference provides a potentially useful integration by the animal given that we can compare it to an objectively-defined need.

Attaining this priority involves comparison of observed patterns of use of cover by deer or elk with patterns predicted on the basis of metabolically-defined need. It thus follows priorities one and two and is necessarily cooperative among all IWIFR projects. The comparison would permit more insightful evaluation of probable consequences to deer or elk of particular forestry practices.

4.4.4 Priority Four: Condition Indices

This priority follows only indirectly from the analysis of thermal cover. Although it is possible to estimate individual energy costs for animals in terms of a common currency (Section 4.1), it is unclear how an animal in the field actually assigns energy to those competing requirements. A condition index related directly to fitness would be most helpful in evaluating how an animal responds to interacting energy costs and gains. McNay and Davies (1985) noted the difficulty in assessing population growth and regulation; Janz et al. (1980) included animal condition in their 'immediate frame of reference'. The concept of some integrative measure of animal health is particularly relevant to elevated costs of thermoregulation because these costs are very likely to be involved in tradeoffs (Section 3.1.3). For example, if an animal is found to be healthy but is known to have experienced thermal stress, then it has been able to compensate through some tradeoff (e.g., abundant forage in a thermally unfavourable environment). Furthermore, it is likely that particular forest structures can meet more than one apparent need (e.g., snow interception, forage production, thermal cover, security cover), and some measure of an animal's overall health as a function of forest structure would be helpful. An analysis refining the material in Appendices 1 through 4 and relating this material to potential condition indices would be useful. It would be particularly helpful to field-testing of models proposed for Phase 2 of IWIFR. The initial approach should take the form of a tightly-focussed problem analysis.

5 SUMMARY

This problem analysis evaluates research priorities for studies which would indicate whether thermal environments in southcoastal British Columbia impose an elevated energy cost for deer and elk and how such energy costs could be modified by forestry practices. Three of the four research priorities can proceed effectively without additional fieldwork; some laboratory research is essential. The greatest utility will be derived if the research is closely cooperative with other projects of IWIFR.

It appears possible to erect an objective definition of thermal cover. Forestry practices influence the major abiotic components determining an animal's operative temperature and therefore modify a stand's ability to provide thermal cover. Use of cover is strongly influenced by animal behaviour, and an objective definition of the effects of thermal cover is essential to distinguish between preference and need. It is probable that requirements or need for thermal cover can be met in stand structures designed to meet other requirements of deer or elk. That is particularly true if those stands provide vegetation 1 to 2 m in height and have a taller, relatively closed canopy nearby. Dense, young stands will be more effective at providing thermal cover than meeting other needs. Given that an objective definition of need is available, documented preference is a useful management tool because it reveals the animal's internal ranking system.

The research proposed will provide relationships that can be generalized for Vancouver Island and the adjacent mainland. It will be more directly applicable to those areas for which other IWIFR projects can provide specific abiotic data. The two research questions of highest priority are: 1) what is the zone of minimum heat production for black-tailed deer; and 2) how do forestry practices influence operative temperature of deer or elk? These questions will be addressed first even though information on heat and mass transfer coefficients are sparse (question 2). Other questions require answers to the two initial questions and close cooperation with other IWIFR projects. The questions concerning preference and condition indices relate more directly to field conditions, integrate more information, and will provide more confidence to predictions regarding the potential impacts of forestry practices on deer and elk.

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APPENDIX 1. Calculation of operative temperature (Te) experienced by an animal (modified from Parker 1983).

$$Te = Ta + (re/\rho cp)Rni, \quad \text{or}$$

$$Te = Ta + re\,\frac{(Rabs - \epsilon_S \sigma Ta^4)}{\rho cp}$$

where: Te = effective or operative temperature (°C),

Ta = air temperature (°C),

re = equivalent resistance to convective and radiative resistances ($s \cdot m^{-1}$),

$Rabs$ = radiation absorbed by the animal ($W \cdot m^{-2}$),

$\epsilon_S \sigma Ta^4$ = (see calculation of radiation fluxes below), and

ρcp = density of the air (ρ) x specific heat (cp) ($1200 J \cdot m^{-3} \cdot {}^\circ K^{-1}$)

Rni = net incoming solar and thermal radiation ($Rabs - \epsilon\ \sigma Ta^4$)

ϵ_S = emissivity of animal's surface

Calculation of radiation fluxes

Net radiation:
σ = Stephan Boltzman constant ($5.67 \times 10^{-8}\ W \cdot m^{-2} \cdot {}^\circ K^{-4}$)

Net radiation = net shortwave radiation - net longwave radiation

Shortwave radiation:

Ap/A = proportion of shadow area (0.3; Campbell 1977: 80)

as = absorptivity to shortwave radiation (0.70 in summer, (0.80 in winter; W.P. Porter pers. comm.)

Spo = solar constant of extraterrestrial flux density = $1360\ W \cdot m^{-2}$

a = scalar incorporating differences between potential direct radiation and solar constant (0.64; Wesley and Lipschutz 1976)

β = scalar incorporating absorption of solar beam by moisture and ozone (0.79; Wesley and Lipschutz 1976)

θ = solar angle (degrees)

Sp = direct beam radiation on surface perpendicular to beam ($W \cdot m^{-2}$)

Sd = diffuse shortwave radiation ($W \cdot m^{-2}$)
If $\theta = 0$, then $Sp = 0$, and $Sd = SW$ as measured

Calculation of θ:

Local apparent time = clock time + longitudinal correction + equation of time (Paltridge and Platt 1976)

$$\text{Sin } \theta = \sin\partial + \sin \text{lat} + \cos\partial(\cos \text{lat}) \cos(15(\text{apparent time} - \text{time of solar noon}))$$

where: ∂ = solar declination, and
lat = latitude.

$$\partial = 0.006918 - 0.399912 \cos\theta r + 0.070257 \sin\theta r - 0.006758 \cos 2\theta r + 0.000907 \sin 2\theta r - 0.002697 \cos 3\theta r + 0.001480 \sin 3\theta r$$

where: θr = solar angle (radians)

$$\text{Sin}\partial = 0.39785 \sin(278.9709 + 0.9856J + 1.9163 \sin(356.6153 + 0.9856J))$$

where: J = Julian day.

$$Eq = 0.000075 + 0.001868 \cos\theta r - 0.032077 \sin\theta r - 0.014615 \cos 2\theta r - 0.040849 \sin 2\theta r$$

where: Eq = equation of time

Longitudinal correction = 4 min for each degree east and -4 min for each degree west of standard meridian.

Total incident shortwave (ST) = incident beam shortwave + diffuse shortwave

$$ST = Sb + Sd$$

$$Sb = (ST - a\beta Spo \sin\theta)/(1 - a)$$

$$Sd = a(\beta Spo \sin\theta - ST)/(1 - a)$$

$$= ST \text{ for } ST < 0.5 \; Spo \sin\theta$$

$Sp = Sb/\sin\theta$

Shortwave radiation (absorbed) = as(Ap/A Sp + 0.5 Sd + 0.5 shortwave radiation up from the ground)

Longwave radiation:

aL = absorptivity to longwave radiation (1.0 for caribou; Monteith 1973)

Longwave down = total radiation flux down - shortwave radiation down

Longwave up = total radiation flux up - shortwave radiation up from the ground

Longwave radiation (absorbed) = aL (0.5 longwave down - 0.5 longwave up)

Rabs = shortwave radiation (absorbed) + longwave radiation (absorbed)

Longwave emitted from animal ($\epsilon_S \sigma Ta^4/\rho cp$)

ϵ_S = emissivity at surface (1.0 for caribou, Monteith 1973)

σ = Stephan Botzmann constant (5.67×10^{-8})

Ta^4 = air temperature in °K = Ta + 273°

$\rho cp = 1200\ J \cdot m^{-3} \cdot {}^{\circ}K^{-1}$

Calculation of equivalent resistance (re):

rr = $\rho cp/4\epsilon_S \sigma Ta^3$ resistance to longwave radiative transfer

d = zero plane of displacement or distance from height zero to average height of heat exchange

= 0.77h where h is average 'crop' height (grass, shrubs, snow)

Zm = momentum roughness parameter for uniform surfaces or length of drag at momentum exchange surfaces
= 0.13 h (see Bussinger (1975) for more complex surfaces)

Z = height of wind measurement

k = von Karman's constant (0.4)

Z' = animal height (assumed to be rib cage)

u^* = friction velocity (u = wind speed, $m \cdot s^{-1}$)

$= u(k)/(\ln(Z + Zm - d)/Zm)$

u = wind speed extrapolated to animal height ($m \cdot s^{-1}$)

$$= \frac{u^*}{k} \ln\left(\frac{Z' - Zm - d}{Zm}\right)$$

rHA = resistance to heat and mass transfer in air for forced convection

$= (307\sqrt{d'/u})\ 0.7$

where d': = characteristic dimension of animal ((length x width)/2), and

0.7 = turbulence factor (G.S. Campbell, pers. comm.)

Resistance to free convection in sun and shade is calculated as

$$rHA_{sun} = 840\ [d/(Ts_{sun} - Ta)]^{1/4}$$

$$rHA_{shade} = 840\ [d/(Ts_{shade} - Ta)]^{1/4}$$

where: Ts = skin temperature measured in sun or shade

$$re = [1/rr + 1/rHA + 0.5\ (1/rHA_{sun}) + 0.5\ (1/rHA_{shade})]^{-1}$$

and $$Te = Ta + re\ \frac{(Rabs - \epsilon_S\ \sigma\ Ta^4)}{\rho cp}$$

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APPENDIX 2. First approximations[a] of daily energy costs (C, $kcal \cdot kg^{-0.75}$) of black-tailed deer and Roosevelt elk by season. Detailed calculations and assumptions are provided in Appendix 4. Tabulated values are C of $M = C\ Wt^{0.75}$

	Spring (1 April-15 June)	Summer/Fall (16 June-30 November)	Winter (1 December-31 March)
Black-tailed deer			
adult female			
maintenance	105	105	105
reproduction			
1 fawn	6-30	53	0-6
2 fawns	6-30	91	0-6
weight recovery	15	13	-
fawn			
maintenance	105	105	152
growth	23	42	-
Roosevelt elk			
adult female			
maintenance	105	105	105
reproduction	11-40	40	40-51
calf			
maintenance	105	105	105
growth	28	46	-

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[a] Does not incorporate specific activity budgets and uses linear rates of weight gain for some calculations (see App. 7.4). See also footnotes of App. 7.3.

APPENDIX 3. First approximations[a] of daily energy costs (C, kcal·kg$^{-0.75}$) of black-tailed deer and Roosevelt elk by season. Detailed calculations and assumptions are provided in Appendix 4. Tabulated values are C of $M = C\ Wt^{0.75}$

	Spring (1 April-15 June)	Summer/Fall (16 June-30 November)	Winter (1 December-31 March)
Black-tailed deer			
adult female			
maintenance[a]	1635	1809	1677
reproduction			
1 fawn	96-472	904[b]	0-96
2 fawns	96-472	1567[b]	0-96
weight recovery	228	228[c]	
fawn			
maintenance[a]	1402[c]	780[c]	1740[c]
growth	310	310	-
Roosevelt elk			
adult female			
maintenance[a]	6818	6818	6818
reproduction	727-2591[d]	2591-2613	2613-3318[e]
calf			
maintenance[a]	4032	2437	3598
growth	1074	1074	-

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[a] Does not incorporate specific activity budgets and uses linear rates of weight gain for some calculations.

[b] Plus an additional cost of 519 kcal·d^{-1} for first 6 days of season.

[c] 24 days only.

[d] Low costs are last trimester of pregnancy; high costs are lactation.

[e] Highest cost borne for 94 days prior to weaning; deer assumed weaned by this period.

APPENDIX 4. Assumptions and calculations used to estimate energy costs of black-tailed deer and Roosevelt elk

Black-tailed deer:

Morphology

- mean adult female weight taken as 45.4 kg from 771 fall eviscerated weights (Hovey 1984) and converted to live weight by the scalar 1/0.69 (Rochelle 1980).

- mean fawn weight derived from same sources using same prodedures to yield 25.8 kg from a sample of 741 fawns. Weights for both age classes may be low; captive 1-year-old black-tailed deer weigh 37-49 kg (K.L. Parker, unpubl.).

- brisket heights of fawns and adult females were taken as 44.8 ($N = 23$) and 53.1 ($N = 25$) cm, respectively, from Jones (1975: 46).

- mean birth weight taken as 3.12 kg; grand mean of 3.29 (Cowan 1956), 3.21 (Golley 1957), 2.99 (Brown 1961), and 3.07 (Cowan and Wood 1955).

'Maintenance' costs

- fall live weights (above) are assumed for beginning of winter; spring maintenance costs assume a 25% overwinter loss of weight (data of Rochelle 1980) (i.e., early spring weight = 0.75 x 45.4 = 34.05 kg); winter weight of adults assumes a linear loss of weight from 45.4 to 34.05 kg over the 121 day period. Fawns are assumed to maintain body weight over winter.

- a conservative activity increment of 1.5 is used in all seasons (e.g., Moen 1973: 356-362).

- daily energetic cost of maintenance is thus 1.5 ($70\ W^{0.75}$) for both adults and fawns. The value of 105 kcal/kg$^{0.75}$ is less than energy required to maintain body weight (ME) as estimated by Seip (1980) for black-tailed deer fawns. He obtained ME estimates of 161 and 152 kcal/kg$^{0.75}$ for early and late fall, respectively. For fawns, we use Seip's value of 152 for the winter period and assume no overwinter weight loss. Growth of fawns was estimated from $Y = 0.0766\ W^{0.71}$ (Robbins 1983: 212) where Y = growth rate (g/day) and W = adult body weight in grams. Assuming 45.4 kg as adult weight, $Y = 155.15$ g/day. Given a birth weight of 3.1 kg, this growth rate produces a 26.5 kg fawn at harvest (150 days later) which compares favourably with the observed value of 25.8 kg.

Reproductive costs

- gestation period for black-tailed deer is 183-212 days (Cowan 1956) with a mean of 203 days (Golley 1957).
- rut occurs from mid-November to early December (Thomas 1970). If mean conception date is November 30, then deer are born about June 22: allocation of gestation period to seasons is then 121 days in winter, 76 in spring, and 6 in summer/fall.
- daily cost of gestation (as % of BMR) = $0.000024\ X^{3.13}$ where X = stage of gestation (%) from Robbins (1983: 177). Thus for winter, daily costs (% of BMR) = 0 to 8.6%. Daily costs for gestation by season allowing for weight changes are: winter - 0 to 96.1 kcal/day; spring - 96.1 to 472 kcals/day; summer/fall - 519 kcal/day for 6 days.
- lactation period of black-tailed deer is taken as 121 days (Sadleir 1980). Based on peak milk yield (Sadleir 1980) the increments over BMR for lactation are 78/70 = 1.11 and 122/70 = 1.74 for 1 and 2 fawns, respectively. Based on average daily yield to 60 days and an energy content of milk of 1.85 kcal/g(Sadleir 1980), the respective increments over BMR are:
  1 fawn $34g/W^{0.75}$ x 1.85 kcal/g = 62.9; 62.9/70 = 0.90
  2 fawns $59g/W^{0.75}$ x 1.85 kcal/g = 109.2; 109.2/70 = 1.56
- Robbins (1983: 187) gave the cost of average daily milk production over 205 days for a 50-kg black-tailed doe with 2 fawns as about 22 $kcal/kg^{0.75}$ or an increment of 0.31.
- we assume weaning by winter (162 days) and daily increments during summer/fall of 0.75 and 1.30 for 1 and 2 fawns, respectively. These increments above BMR for a 162-day period are less than Sadleir's for peak milk yield or yield to 60 days, but greater than Robbins' estimate to 205 days. Total costs of reproduction allowing for weight change are (kcal/day):

	spring	summer/fall	winter
Gestation	96 - 472	-	0 - 96
Lactation		904 - 1568	

Weight recovery and growth

- for adults assume 25% overwinter weight loss (Rochelle 1980): 45.4 x 0.75 = 34.05 kg adult female; a loss of 11.4 kg.

- energy requirements for growth are 1 to 3 kcal/g (Robbins 1983: 215) - assume 2 kcal/g.

- 11,400 (2) = 22,800 kcals required.

- assume 100 days to recover weight (by July 9) or 228 kcals/day.

- average metabolic weight over entire period of gain = (45.4 + 34.05)/2 or 39.7 kg = 15.8 $kg^{0.75}$ (Mautz 1978: 347). For the entire period of gain the increment over BMR associated with the costs of growth is: 288/15.8 = 18.2 $kcal/kg^{0.75}$; 18.2/70 = 0.26. Increments in App. 2 are further refined by season.

- for fawns assume the growth rate of 155.15 g/day noted earlier except during winter when the higher value for maintenance is elected and no weight loss occurs (see discussion of 'maintenance').

- estimated cost of growth is obtained from Robbins (1983: 219) using $Y = 0.76\ W^{0.37}$ where Y = kcal/g of weight gain and W = body weight. During summer/fall $Y = 0.76\ ((25.8 + 3.12)/2)^{0.37}$ = 2.04 kcal/g; similar to the estimate of 2 kcal/g employed earlier. We assume 2 kcal/g throughout. Thus weight gain costs 155.15 x 2 = 310.3 kcal/day.

Average weights incorporating weight changes are:
   Fawn -
    (31.2 + 25.8)/2 = 14.5 kg during summer/fall; 25.8 kg through winter; and 31.7 kg during spring ((25.8 + (25.8 + 76 x 0.155))/2).
   Adult female -
    (42.7 + 45.4)/2 = 44 kg during summer/fall; (45.4 + 34.05)/2 = 39.7 during winter; and (34.05 + 42.7)/2 = 38.4 during spring. Spring and summer growth assume a growth rate of 114 g/day, or a period of 100 days from the end of winter to recover weight loss.

Respective increments over BMR for growth of fawns are thus: zero in winter; 0.60 in summer/fall (310 kcal/day; $\bar{x}$ weight = 14.5 kg; $W^{0.75}$ = 7.43 kg; 310/7.43 = 41.72; 41.7/70 = 0.60); and 0.33 in the following spring (calculation procedure identical but $W^{0.75}$ = 13.36 kg as W = 31.7 kg).

Roosevelt elk:

Morphology

- mean adult and yearling female live weights taken as 216 and 169 kg, respectively (Blood and Smith 1984).
- Birth weight taken as 16.8 kg (Morrison *et al*. 1959 for *C. elaphus nelsoni*).

- brisket height (Y) calculated from data for *C.e. nelsoni*: $Y = 26.18\ [\ln(x+1)]^{0.65}$
where: x = body weight in kg (from Parker *et al*. 1984: 479). Calculated brisket height of adult female is 78.1 cm.

'Maintenance' costs

- because little is known about Roosevelt elk weight changes, adult female weight is assumed to remain constant throughout the year. The increment over BMR is the same as for black-tailed deer (1.5 in all seasons), thus the energy cost is 1.5 x 70 = 105 $\text{kcal}\cdot\text{kg}^{-0.75}$ or 6818 $\text{kcal}\cdot\text{d}^{-1}$.

- the use of same increment in all seasons may overestimate relative energy costs during winter. The value of 105, however, is lower than the 153 $\text{kcal}\cdot\text{kg}^{-0.75}$ estimated by Mould and Robbins (1981) as necessary to maintain positive nitrogen balance. The same increment is used for calves.

- growth rate of calves (Y, $\text{g}\cdot\text{d}^{-1}$) was estimated from
$Y = 0.0766W^{0.71}$ from Robbins (1983: 212)
where: W = adult weight in grams. Estimated growth rate was 537.1 g/d. This value is within the range of 454 $\text{g}\cdot\text{d}^{-1}$ over 53 days and 625 $\text{g}\cdot\text{d}^{-1}$ over 141 days reported for *C.e. nelsoni* by Moran (1970 and pers. comm. in Bubeník 1982: 130).

Reproductive costs

- gestation period for elk has been estimated at 247 to 262 days (Johnson 1951, Morrison *et al*. 1959, Harper *et al*. 1967). A period of 250 days is assumed (Harper 1971). These days were allocated to seasons by assuming cows were bred on October 1 (Morrison *et al*. 1959; Prothero *et al*. 1979): 61 days in summer/fall, 121 days in winter, and 68 days in spring. Calves are thus born on June 7.

- daily costs of gestation are estimated from Robbins

(1983: 177) cost (% BMR) = $0.000024X^{3.13}$, where x = stage of gestation in %. The increments per season are thus: 0.005 for summer/fall, 0.005 to 0.16 for winter, and 0.16 to 0.44 in spring. Maximum cost as kcals/day in spring is therefore 0.44 x 70 ($261^{0.75}$) = 2000 kcals/day.

- length of lactation is reported as 150 days (Bubenik 1982: 173) and 280 days (Robbins 1983: 187). Robbins' estimate is used which yields an increment of 0.57 $\mathrm{kcal\cdot kg^{0\ 75}}$ (Robbins 1983: 187). Because most of the energy costs of lactation occur during the first 60 days, this increment averaged over 280 days is likely to be unrealistically lower for the summer/fall period (App. 2 and 3).

Growth of calf

- growth rates were estimated at 537 $\mathrm{g\cdot d^{-1}}$ (see maintenance). At that growth rate calves in fall harvest (150 days after birth) would weigh 97.4 kg. By mid-December calves would weigh 119.4 kg which compares favourably with 117 kg reported for *C.e. nelsoni* calves in December (Greer 1967 in Taber *et al*. 1982). Assuming no weight change over winter, calves at their first birthday would weigh 147.8 kg. This estimate is lower than the mean weight of two young female Roosevelt elk (169 kg for 9- and 11-month-old animals; Blood and Smith 1984), but is greater than weights of Rocky Mounain elk of similar ages (Greer 1965, 1966; K.L. Parker unpubl.).

- energy required for growth was calculated assuming 2 kcal/g weight gain, as for black-tailed deer. Costs per day are thus 1074 kcal. Assuming that weight change is linear, mean weight in the summer/fall is (21.1 + 111.3)/2 = 66.2 kg or 23.2 $\mathrm{kg^{0.75}}$. Costs per day in summer/fall are thus 1074/23.2 = 46.3 $\mathrm{kcal\cdot kg^{-0.75}}$.

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